ECOLOGICAL SEPARATION OF *ANOLIS* LIZARDS IN A COSTA RICAN RAIN FOREST

BY

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Abstract of Dissertation Presented to the Graduate Council
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ECOLOGICAL SEPARATION OF *ANOLIS* LIZARDS IN A COSTA RICAN RAIN FOREST

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Ecological separation in eight sympatric congeneric lizard species in the genus *Anolis* was studied at Río Frío, a site in a lowland tropical rain forest on Costa Rica's Caribbean slope. Four aspects of the ecology of the Río Frío anoles are considered: (1) body size, (2) food, (3) reproduction, and (4) population size and structure.

Size and prey patterns have been thoroughly described for island anoles by other authors, but the Río Frío anole community contains more species in a single habitat than do the island communities. In many respects, these lizards show size-prey patterns similar to island anoles, e.g. ecological separation is achieved primarily through spatial differences, both vertical and horizontal, and size difference. But in contrast, differences in mainland anoles are not as clear-cut, large male size is found in only two species, body size differences are reduced, and prey size

differences are generally less than would be found within or between island species.

Anoles that live without congeners on islands tend toward certain size patterns. At Río Frío, it was found that anoles which are restricted to peripheral habitats, e.g. streamside or exposed canopy, are little influenced by congeners, and show the same size, sexual dimorphism and prey size patterns as do solitary island anoles.

Anoles collected in May, just after the dry weason, weigh less at any length than those collected at other times. That this is a result of dry season food stress, due to reduced populations of small arthropods, is further corroborated by the finding that lizards collected in May frequently had not eaten.

Reproduction in Río Frío *Anolis* is continuous throughout the year. There is some variation in some species, apparently in response to environmental change, but in none is there a complete cessation of reproduction. Young are present in all seasons.

Density of low bush and ground amphibians and reptiles at Río Frío was estimated from fenced quadrats. For all species collected, density is 3752-5378 individuals/ha; for *Anolis* alone, the estimate is 688-1252 anoles/ha. Anoles had a combined estimated biomass of 422-1026 g/ha.

I. GENERAL INTRODUCTION

This study concerns the ecology of the lizards of the genus *Anolis* at a site in the lowland rain forest on Costa Rica's Caribbean slope. Anoles are generally small, arboreal, insectivorous lizards that make up a large, important part of the fauna of the American tropics. In some areas, usually near the geographic or climatic limits of the genus *Anolis*, only a single species may be found, but in the rain forests many species co-exist. Río Frío, the site of this study, was chosen because at least eight species of anoles live in close contact, apparently dividing their resources--space, food, time, etc.--in a way that minimizes, without altogether avoiding, the evolutionary friction of competition.

Río Frío is the Standard Fruit Company's name for a very large banana plantation. When I first visited there, most of the area was rain forest, slightly disturbed and with some second growth, but basically mature forest. The banana company was in the process of cutting the forest and replacing it with bananas. Most of the lizards collected for this study were taken as the trees were felled; a few were collected in still undisturbed areas. When I last visited Río Frío in May 1970, about two-thirds of the area had been cleared of forest, and banana production was in full operation. At the time of this writing, early 1979, the forest and most of its animal inhabitants are gone.

So this study is about the ecological separation of the anoles in a rain forest that used to be. Its conclusions do apply, I believe, to the increasingly diminishing patches of Costa Rican rain forest that remain.

Four aspects of the ecology of the Río Frío anoles are considered here: (1) body size, (2) food, (3) reproduction and (4) population size and structure. Because of the distinctness of the sections, each will have its own, more specific introduction.

II. DESCRIPTION OF THE STUDY AREA

Río Frío is located at 10° 20' N, 83° 53' W in Heredia Province, Costa Rica (Fig. 2-1). It is approximately 18 km SE of Puerto Viejo and 16 km NW of Guapiles, and has an elevation of approximately 100 M. All collections were made on land belonging to the Standard Fruit Company, now a large banana plantation. Most of my specimens were collected in the area between the Río Sucio and the Río Chirripó. Population quadrat collections were made on the NW side of the Río Sucio.

Río Frío is on a relatively flat alluvial plain below the Cordillera Central. The area is shown as Premontane Wet Forest, basal belt transition, on the Holdridge Life Zone map of Tosi (1969), but rainfall data for 1961-65 (Table 2-1, Figure 2-2) show more than 4000 mm of precipitation. This would indicate a Holdridge Life Zone classification of Tropical Wet Forest. The vegetation appeared to fit the description (Holdridge et al., 1971) of Tropical Wet Forest more closely than Premontane Wet Forest (Table 2-2). For a more detailed description of a very similar forest, see the description of Finca La Selva (Holdridge et al., 1971) which is located about 10 km from Río Frío.

While collections were being made at Río Frío, the forest was being replaced by bananas in the following sequence:

1. Selected trees were harvested for lumber. This involved relatively few trees and caused no

appreciable difference in the structure of the forest.

2. Some time after this lumbering (as long as many months in some areas), bananas were planted in the forest.
3. One to a few days after the bananas were planted, all trees were felled and left to rot.
4. Bananas grew up among the rotting trees, and second growth was cut back.

Most of my specimens were collected as the trees were felled in step 3 above. Population quadrat collections were made in an area that had been lumbered (step 1 above) many months previously, but had not been otherwise disturbed. No attempt was made to census or collect anoles in areas after the forest was replaced by bananas.

It is generally accepted that wet tropical forests are wet the year around, at least from a temperate point of view. La Selva/Los Diamantes receives as much rain during the three driest months, January through March, as Illinois does in an entire year. Nevertheless, Río Frío does have seasonality of rainfall (Fig. 2-2). The wet season extends from May through December, and the dry season from January through April. The wet season has a characteristic rainfall depression, called locally the *veranillo*, in late August and early September. Even during this period, the forest usually receives regular rainfall, and the forest floor is continuously damp. During the dry season, however, there may be several days or even a week or more with very little or no rain. Occasionally, the dry season is interrupted by a period of rain, such as occurred during February 1970. At Río Frío, 495 mm of rain fell during the 13 days from 5 February through 17 February, with only one of these days receiving no rain. In contrast, the other 15 days of February received only 24 mm of rain. Because rainfall data for Río Frío were not kept prior to December 1969, the average data from Puerto Viejo (18 km NW) and Los Diamantes (15 km SE) are used.

Day length at the latitude of Río Frío (Fig. 2-2) ranges from 12 hours, 42 minutes at the end of June to 11 hours, 32 minutes in mid-December, a total variation of only 1 hour, 10 minutes (List. 1966).

Seasonal temperature variation is shown in Figure 2-3 and Table 2-3. Again, Río Frío data are available only after December, 1969. For a typical annual pattern, the Puerto Viejo/Los Diamantes average is shown.

Anoles were collected during four periods (Fig. 2-2): (1) September and early October, a dry period (*veranillo*) during the wet season; (2) November and early December, the very wet, last part of the wet season; (3) February and early March, the driest part of the dry season; and (4) early May, the last of the dry season or beginning of the wet season. These four periods will be designated hereinafter simply as September, November, February and May respectively. A few anoles of some of the less abundant species were collected during the preceding August and are used in some sections.

The fauna of lowland tropical forests is distinguished for its diversity, and the forest at Río Frío was no exception. Many other animals interact with the anoles as predators, prey, or competitors. Predators include snakes, birds, small mammals and occasionally larger lizards. Prey items include most of the huge number of insect species, spiders, snails, smaller lizards or frogs, and almost any other moving invertebrate of appropriate size. Chief competitors, for food at least, are probably birds and frogs, and possibly spiders; and not other lizards. Most other lizards at Río Frío are either nocturnal or herbivorous, or are found primarily in second growth (Table 2-4). Thus, the most prominent lizard competitors of anoles are other anoles.

TABLE 2-1. Average Monthly Rainfall

MONTH	PUERTO VIEJO	LOS DIAMANTES	PUERTO VIEJO AND LA SELVA AVERAGE
July	522.0	517.1	520
August	417.0	326.3	372
September	270.0	388.6	329
October	385.7	505.0	445
November	418.4	557.5	488
December	477.2	544.2	511
January	324.4	196.3	260
February	174.6	134.3	154
March	198.3	231.5	215
April	259.7	202.0	231
May	399.8	375.1	387
June	425.3	407.4	416
Total	4272.4	4385.3	4328

NOTE: Average monthly rainfall (mm) for the years 1961-65 at Puerto Viejo and Los Diamantes, the two weather stations closest to Río Frío.

TABLE 2-2.
Comparison of Tropical Premontane Wet Forest and Tropical Wet Forest Vegetation

Tropical Wet Forest

General. Tall, multistratal evergreen forest. A few canopy species are briefly deciduous, usually when flowering, but this does not affect the evergreen aspect of the forest as a whole. Number of tree species very large.

Upper canopy. Trees 45-55 m tall, with occasional larger emergents; crowns round to umbrella-shaped, usually not in lateral contact with each other. Clear holes up to 30 m long and 125-200 cm in diameter. Smooth, thin, light-colored bark and high buttresses very common, but trees lacking buttresses or with dark, rough, flaking or lissured bark also occur. Leaves elliptical, usually lacking lobes or teeth, often glossy, mostly less than 10 cm long.

Lower canopy. Trees 30-40 m tall, filling spaces between upper canopy trees. Crowns round, trunks mostly slender, lacking large buttresses. Bark dark or light, mostly smooth.

Understory. Trees 10-25 m tall, dense, commonly with narrow conical crowns and slender stems, often leaning, twisted or crooked, usually with smooth dark bark; flowers and fruits sometimes produced directly from the trunk and lower branches (cauliflory). Leaves or leaflets relatively large (up to 20 cm long), elliptical, long, pointed tips ("drip tips"). Stilt-rooted palms often abundant.

Shrub layer. Dwarf palms, often with undivided leaves, usually abundant, mostly 1.5-2.5 m tall. Miniature trees with unbranched main stems present but usually less common. Giant herbs with banana-like leaves often prevalent, especially in clearings and disturbed places.

Ground layer. Often bare, or with a few ferns, Selaginellas, or tree seedlings.

Epiphytes. Including orchids, bromeliads, and large-leafed herbaceous climbers (aroids, Cyclanthaccae) common but often not conspicuous; moss layer on tree trunks very thin or lacking. Large bush ropes uncommon; epiphytic shrubs and strangling trees mostly rare.

Tropical Wet Forest is distinguished from Premontane Wet Forest by (1) larger buttresses of canopy trees; (2) larger trunk volumes, especially in canopy trees; (3) bark generally smoother; (4) palms much more common in understory and shrub strata; (5) tree ferns less common; (6) more tree species per 0.1 ha; (7) physiognomic differences between Tropical Wet and Premontane Wet communities are subtle, but there are consistent differences in floristic composition useful to the specialist; (8) more luxuriant appearance than forests at higher elevations, which feel cooler, darker, and more gloomy. (These subjective impressions, of course, may not be shared by some observers.)

TABLE 2-2 - extended

Tropical Premontane Wet Forest

General. Tall to intermediate semi-evergreen forest with two or three tree strata; emergent, canopy, and subcanopy not always readily distinguished. In exceptionally dry years or on edaphically dry sites, most canopy species may drop their leaves for a few weeks. A few species are always dry-season deciduous. The subcanopy, small trees, and shrub layers are evergreen.

Canopy. Trees mostly 30-40 m tall (with occasional emergents up to 50 or 55 m), mostly with round to spreading crowns and slender to stout trunks with clear lengths of 25 m or less. Buttresses are common but much smaller than in Tropical Moist and Wet forests, except in warm transitional areas. Bark mostly brown or gray, moderately thick, flaking or fissured, but smooth and light-colored in a few species. Leaves are mostly simple, elliptic, glossy, 5-10 cm long, with entire or minutely toothed margins, often somewhat crowded at the tips of the branches. Number of species large.

Small tree stratum. Composed of a dense layer 10-20 m tall of sapling canopy trees mixed with small, slender-trunked trees having relatively deep crowns and smooth, often dark bark. Stilt roots and long, strapshaped leaves are common. Tree ferns are occasional; stilt-rooted palms occur in warm transitional areas.

Shrub layer. A dense stratum of single-stemmed "miniature" trees and young canopy trees 2-3 m tall. Small palms are generally rare or lacking, but are abundant in warm transitional areas.

Ground layer. Generally bare except for ferns, which may be abundant (especially along trails), and tree seedlings.

Epiphytes. Orchids and bromeliads mostly not conspicuous; herbaceous vines are common, mostly climbing the larger trees. A thick layer of moss covers the tree trunks.

Premontane Wet Forest is distinguished from Tropical Wet Forest by (1) much lower frequency of palms in small tree and shrub strata; (2) higher frequency of tree ferns; (3) smaller buttresses in canopy trees, high buttresses rare; (4) bark generally somewhat rougher; (5) trunk and crown volume of canopy trees somewhat smaller; (6) fewer tree species per 0.1 ha.

SOURCE: Holdridge et al., 1971.

TABLE 2-3. Average Daily Temperature

MONTH	PUERTO VIEJO		LOS DIAMANTES		PUERTO VIEJO AND LOS DIAMANTES MEAN		RIO FRIO	
	MAX.	MIN.	MAX.	MIN.	MAX.	MIN.	MAX.	MIN.
JAN	31.8	20.5	28.1	19.3	30.0	19.9	25.1	22.0
FEB	31.4	20.2	29.2	20.7	30.3	20.5	24.2	21.4
MAR	31.2	20.2	29.0	19.9	30.1	20.1	26.7	21.9
APR	33.3	21.7	30.2	21.7	31.8	21.7	29.8	22.0
MAY	35.2	21.0	31.6	21.3	33.4	21.2	28.9	21.3
JUN	35.1	21.0	32.5	21.4	33.8	21.2	29.2	22.5
JUL	34.2	20.9	30.9	21.4	32.6	21.2		
AUG		21.0	31.4	21.1	21.4	21.1		
SEP	33.9	21.2	30.7	20.6	32.3	20.9		
OCT	33.9	20.4	31.2	20.7	32.6	20.6		
NOV	32.1	19.8	28.6	19.9	30.4	19.9		
DEC	29.2	19.7	27.6	20.5	28.4	20.1	26.0	22.3

NOTE: Average daily maximum and minimum temperatures (^{o}C) for 1966 at Puerto Viejo and Los Diamantes, the two weather stations closest to Río Frío.

TABLE 2-4. Other Lizards at Río Frío

Anguidae	
Celestus sp.	nocturnal (?), arboreal
Diploglossus monotropis	nocturnal (?), terrestrial
Gekkonidae	
Lepidoblepharis xanthostigma	nocturnal, terrestrial
Sphaerodactylus spp.	nocturnal, arboreal
Thecodactylus rapicauda	nocturnal, arboreal
Iguanidae	
(*Anolis* - 8 species)	
Basiliscus plumifrons	diurnal, arboreal, riparian
Basiliscus vittatus	diurnal, terrestrial, riparian
Corytophanes cristatus	diurnal, low arboreal
Iguana iguana	diurnal, arboreal, riparian
Polychrus gutturosus	diurnal, high arboreal
Scincidae	
Leiolopisma cherriei	diurnal, terrestrial
Mabuya unimarginata	diurnal, terrestrial, clearings
Teidae	
Ameiva spp.	diurnal, terrestrial, clearings
Xantusidae	
Lepidophyma flavimaculatum	nocturnal, terrestrial

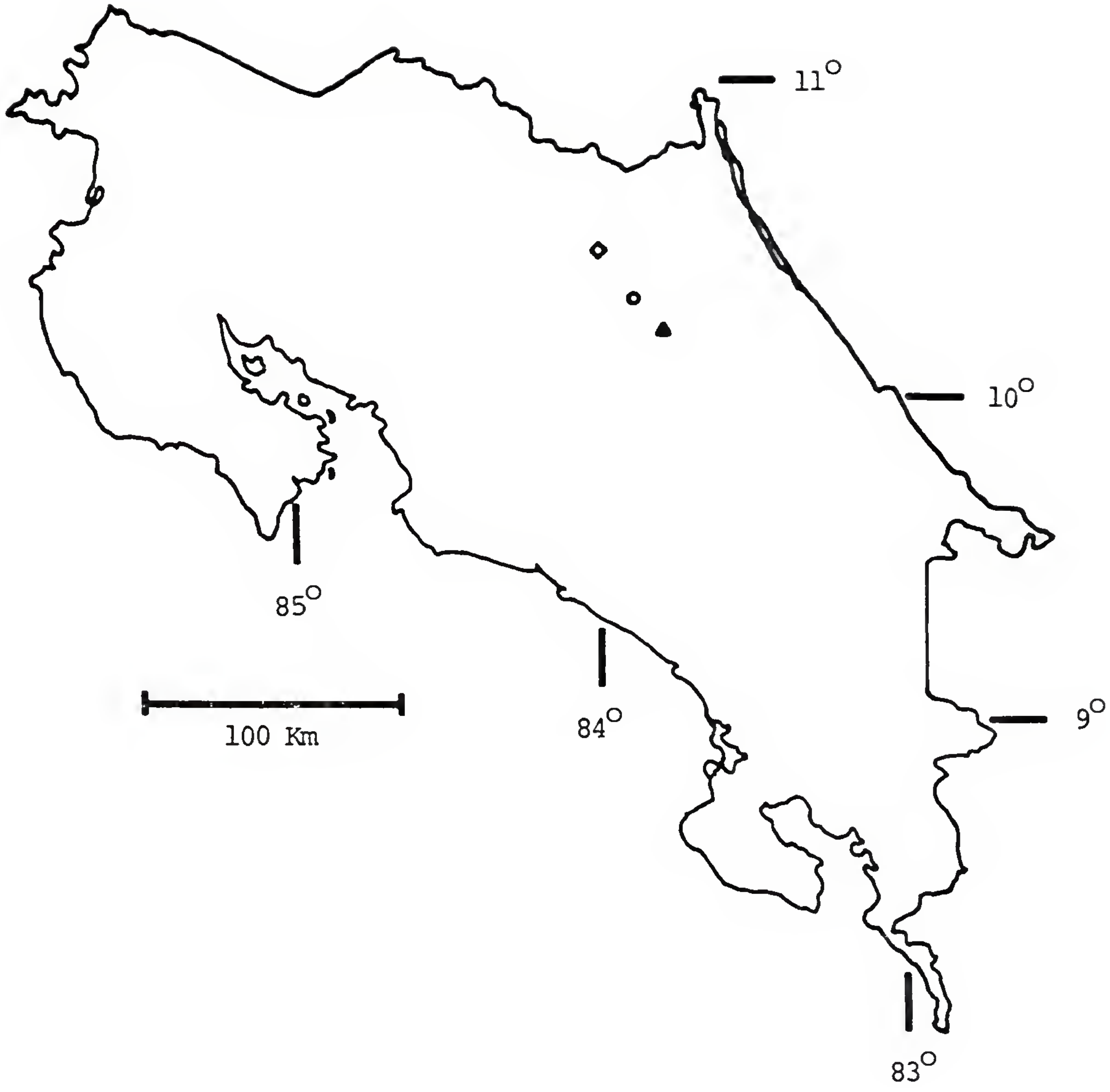


FIGURE 2-1. Map of Costa Rica. Shown are the location of Río Frío (circle), a Standard Fruit Company banana plantation, and the two nearest towns that are on most maps: Puerto Viejo (diamond) and Guapiles (triangle).

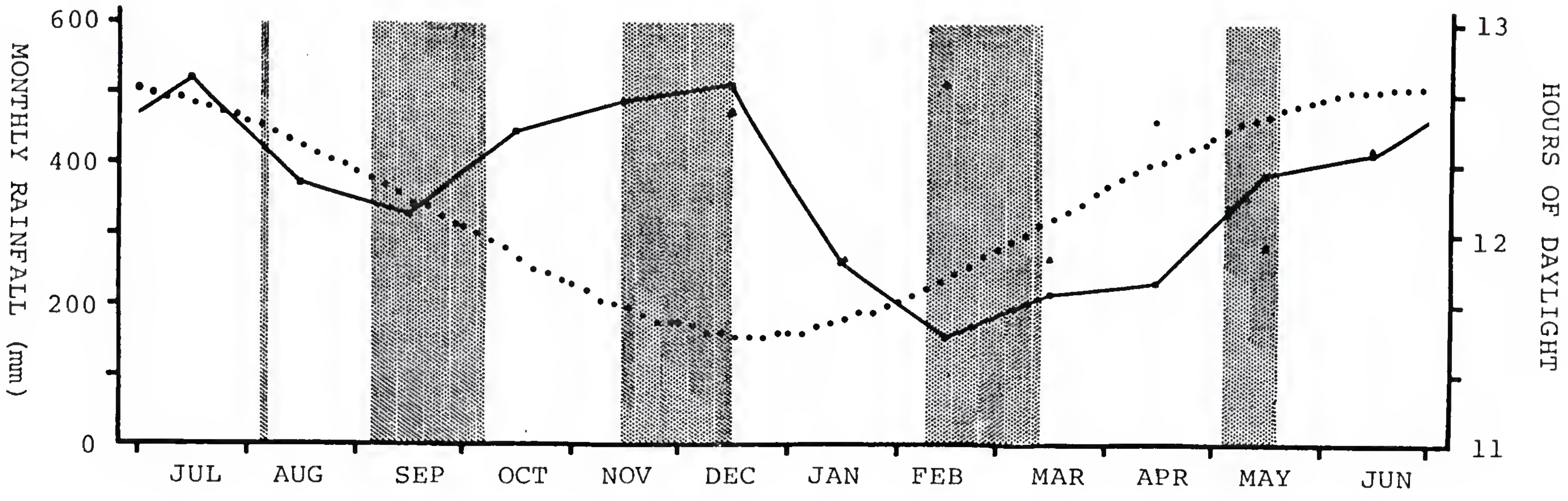


FIGURE 2-2. Rainfall and Day Length for Río Frío. Rainfall (solid line) given as means of the total monthly rainfall for the years 1961-1965. Values are the averages of those of Puerto Viejo and Los Diamantes. Monthly total rainfall at Río Frío, from December 1969 to June 1970, is indicated by triangles. Day length (dotted line) values are from the tables for 10 20' N (Río Frío) of List (1966). Shaded areas indicate collecting periods.

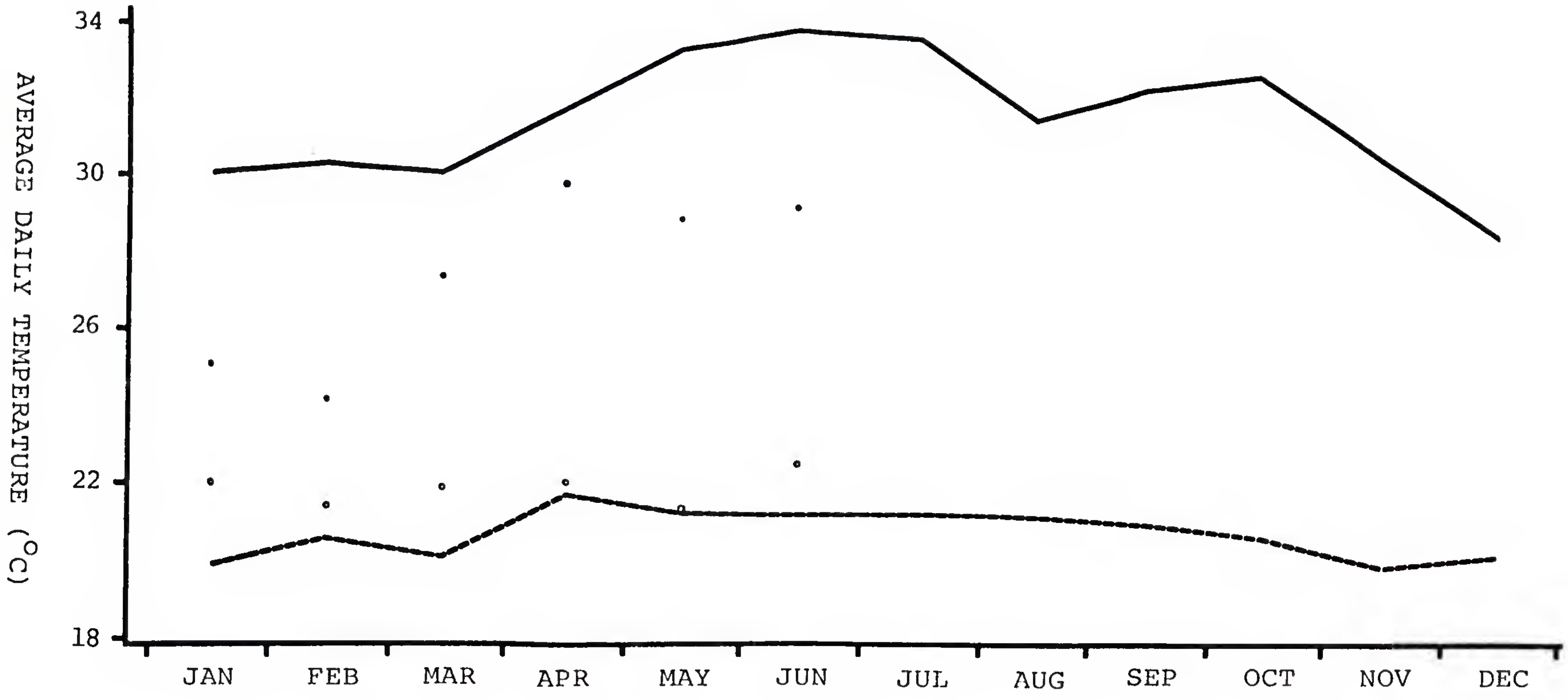


FIGURE 2-3. Average Temperatures for Río Frío. Average daily maximum (solid line) and minimum (dashed lined) temperature (C). Values are the averages of those of Puerto Viejo and Los Diamantes. Monthly averages of Río Frío (December 1969 to June 1970) are indicated by dots (maxima) and circles (minima).

III. DESCRIPTION OF THE ANOLES

Part of the rationale for studying ecological interactions among sympatric congeners is that, being very close in an evolutionary sense, they should show intense and, therefore, important competition. In this study, ecological relationships of eight species of the large iguanid genus *Anolis* are discussed. These eight species, although diverse in their ecological niches, are very close phyletically.

The anoles are a group of over 200 iguanid species, the distribution of which centers in the American tropics and extends into the subtropics. All eight species of anoles present at Río Frío belong to what Etheridge (1960) and others have termed the Beta Section, as species derived from Central American ancestry are designated (in contrast to the Alpha or South American derived species). Three species groups, designated as series by Etheridge (1960), are represented: *petersi* series (*A. biporcatus, A. capito* and *A. pentaprion*), *fuscoauratus* series (*A. carpenteri, A. limifrons* and *A. lionotus*) and *chrysolepis* series (*A. humilis* and *A lemurinus*). Etheridge (1960) suggested that the *petersi* series of large lizards is a relatively primitive group, and that the *fuscoauratus* series and *chrysolepis* series are its more advanced descendants.

The size, shape, color and gross habitat distribution are ecologically important attributes of anoles. Some of these will be discussed more thoroughly in later sections, but in order to help the reader visualize these characteristics in the eight species discussed here, a brief summary is given below.

Anolis humilis is the smallest and most numerous anole at Río Frío. Maximum snout-vent length (SVL) is only 40 mm in my samples, although Fitch (1975) found them up to 43 mm, and maximum weight is 1.7 g. *A. humilis* is a stout-bodied anole of more or less uniform brown dorsal color; females occasionally have a light stripe or a rhomboid pattern on the back. Males have a relatively large dewlap, red bordered with yellow, while females lack a dewlap, but may have a small patch of red on the throat. *A. humilis* is usually found close to the ground; Fitch (1975) found 92% on the ground or below 20 cm. They rarely go above 50 cm on a tree trunk, even when chased.

Anolis lemurinus, the second member of the *chrysolepis* series, is considerably larger than *A. humilis*. My largest specimen has a 60 mm SVL, and the heaviest is 5.06 g. Taylor (1956) describes a specimen with a 63.5 mm SVL. Also a stout-bodied anole, *A. lemurinus* is dark gray in color usually with a blotched dorsal pattern; females may have a light band or a series of diamonds on the dorsal midline. Males have a relatively small dewlap, deep red in color, lighter at the edge. The female dewlap is very small, but colored like that of the male. *A. lemurinus* is found on the trunks of large trees, usually on the lower part of the trunk, but when disturbed will flee quite high.

Anolis limifrons is a slender, gray anole that is second only to *A. humilis* in abundance at Río Frío. Slightly longer than *A. humilis, A. limifrons* has a maximum SVL of 42 mm in the Río Frío collection; Fitch (1975) lists 45 mm as the maximum. Maximum weight in the Río Frío sample was 1.5 g; Fitch (1975) gives 1.7 g. Males are more or less uniform light gray, lighter on the venter having a small white dewlap with an orange spot in its center. Females are colored like the males, or with a light dorsal band or diamond pattern. Females lack a dewlap. *A. limifrons* is a shrub-level anole usually found on vertical trunks of shrubs, saplings or larger trees, almost always between 0.5 and 2 m above the ground. Fitch (1975) found 87.3% of this species perching above ground level, with a mean perch height of 0.78 m. More than any other Río Frío anole, *A. limifrons* is found commonly in second growth and disturbed areas, but is still more abundant in less-disturbed forest.

Anolis carpenteri is closely related to *A. limifrons*, and is virtually the same length. The longest Río Frío specimen is 43.5 mm SVL; Fitch (1975) records it up to 45 mm SVL. It is slightly more slender than *A. limifrons*, with the heaviest *A. carpenteri* weighing only 1.2 g. *A. carpenteri*, which was not described until 1971 (Echelle, Echelle and Fitch), is a very cryptic, lichen-green anole with a light half-ring below the eye and a white venter. Males have a large bright orange dewlap; females lack a dewlap but may have a trace of orange pigment on the throat. The habitat of *A. carpenteri* is problematic. Fitch and his co-workers (Echelle, Echelle and Fitch, 1971; Fitch, 1975) found their first ten specimens on lichen-covered rocks at ground level in the Tropical Moist Forest, premontane transition Life Zone. They then obtained 14 more lizards in 10 months at Finca La Selva in the Premontane Wet Forest, basal belt transition Life Zone. Of these 14, only 5 were from undisturbed rain forest; the rest were from cacao or palm groves. Five of these lizards were found at ground level, three on tree bases and two in leaf litter. Fitch (1975) states that all were "on or near lichen-mantled tree trunk or log which provided concealing background," and that three of fourteen recorded "dropped to the ground almost immediately after being flushed." When I first visited Río Frío in August 1969, I found *A. carpenteri* to be very common among the just-felled trees. In fact, *A. carpenteri* was so common that I collected several, decided it was a common species that I didn't recognize, and released them all. Only after a later conversation with N. J. Scott, did I realize that the species was probably then undescribed. *A. carpenteri* was also quite common among the cut trees in September and October, but less common in November, December, February and March. None were seen in May. Only one specimen, a 26 mm SVL ♂ was collected outside the area of newly felled trees. This individual was collected from a small sapling after it had been flushed out from a liana about 2.5 m above the ground.

I would suggest that the apparent rareness of *A. carpenteri* reflects its preference for lichen-covered perches, probably at moderate heights. The few specimens found on the ground (with the exception of the type series) are there because of a "drop-and-freeze" escape behavior. While not as common as *A. limifrons* or *A. humilis,* it is like several other rain forest reptiles (for example, see Corn, 1974), only encountered when disturbed from its high arboreal habitat.

A. lionotus is the largest anole of the Río Frío *fuscoauratus* series, and the most restricted in habitat. It is never found more than a few meters from the edge of a river or stream. These lizards perch on the bare bank, rocks, debris and occasionally on vegetation. When disturbed, they hide under debris, or readily enter the water, where they swim and hide under submerged material. The largest Río Frío *A. lionotus* is 71 mm SVL, weighing 6.6 g. Fitch (1975) found much larger specimens, up to 85 mm SVL and 13.7 g. The color of both sexes is chocolate-brown with cream-colored lateral stripes and a lighter venter. Males have a large, pale orange dewlap, which females lack.

Anolis capito is a rare, large anole. The largest Río Frío specimen was 87 mm SVL, weighing 13.0 g. Both Fitch (1975) and Andrews (1971a) found them as long as 95 mm SVL. The color of *A. capito* is a mottled olive-green to brown. Females occasionally have a distinct brown mid-dorsal stripe. The male dewlap is very small and greenish-white; an even smaller, similarly colored dewlap occurs on females.

A. capito is found on the ground or on tree trunk bases or buttresses, usually lower than 1 m. Escape behavior involves freezing, or, occasionally, running across the ground or onto a tree trunk, never higher than two meters or so. *A. capito* was probably much more common at Río Frío than my collecting suggests, but its escape behavior made it very difficult to find in the newly felled trees.

Anolis biporcatus is the largest Río Frío anole, reaching 93.5 mm SVL, and weighing up to 20.0 g. Taylor (1956) states that the maximum SVL is 102 mm. Dorsal color can be changed from bright green through medium brown in both sexes. The male dewlap is large, with a bright blue center and an orange-red outer portion. The dewlap of the female is smaller. *A. biporcatus* is a tree anole, found from lower sections of trunks to high in the crown.

Anolis pentaprion is a moderately large, short-legged anole. My longest specimen is 66.5 mm SVL, and the heaviest 4.3 g; Taylor (1956) and Fitch (1975) examined a specimen of 75 mm SVL. Dorsal coloration is light gray sometimes mottled with dark patches. The dewlap is large and deep purplish-red in color. The dewlap of the female is only slightly smaller than that of the male. The tail is relatively short and somewhat prehensile. *A. pentaprion* is the only truly open-habitat heliotherm among the eight Río Frío anoles. Most specimens were found on exposed tree trunks in open country or high in the crowns of forest trees. All of mine were taken from just-felled trees. In forests *A. pentaprion* probably spends most of its time high in the leaves and twigs, where it can bask, or at least take advantage of the higher temperatures of the exposed tree crown. Campbell (1971) obtained a mean of 33° C for 12 records of *A. pentaprion* in a thermal gradient. The short legs and prehensile tail are undoubtedly adaptations for movement on small twigs and branches.

From the preceding descriptions, it can be seen that the eight anole species at Río Frío are well distributed throughout the habitat, with some important separation, both vertically and horizontally (Fig. 3-1). *Anolis capito, A. humilis* and *A. lionotus* form a group of highly terrestrial species, with *A. humilis* and *A. capito* restricted to forest floor and tree bases, and *A. lionotus* almost completely separated from all other anoles in its riparian habitat. *A. biporcatus* and *A. lemurinus* are usually found on tree trunks of moderate to large size, and only rarely elsewhere. *A. limifrons* occurs on a rather broad spectrum of perches, from ground to moderately high trunks, but is primarily found in the shrub layer. *A. pentaprion* and *A. carpenteri* occupy the highest habitats, with *A. pentaprion* preferring the sunny crown and *A. carpenteri* restricted to dark, lichen-covered trunks, branches and lianas.

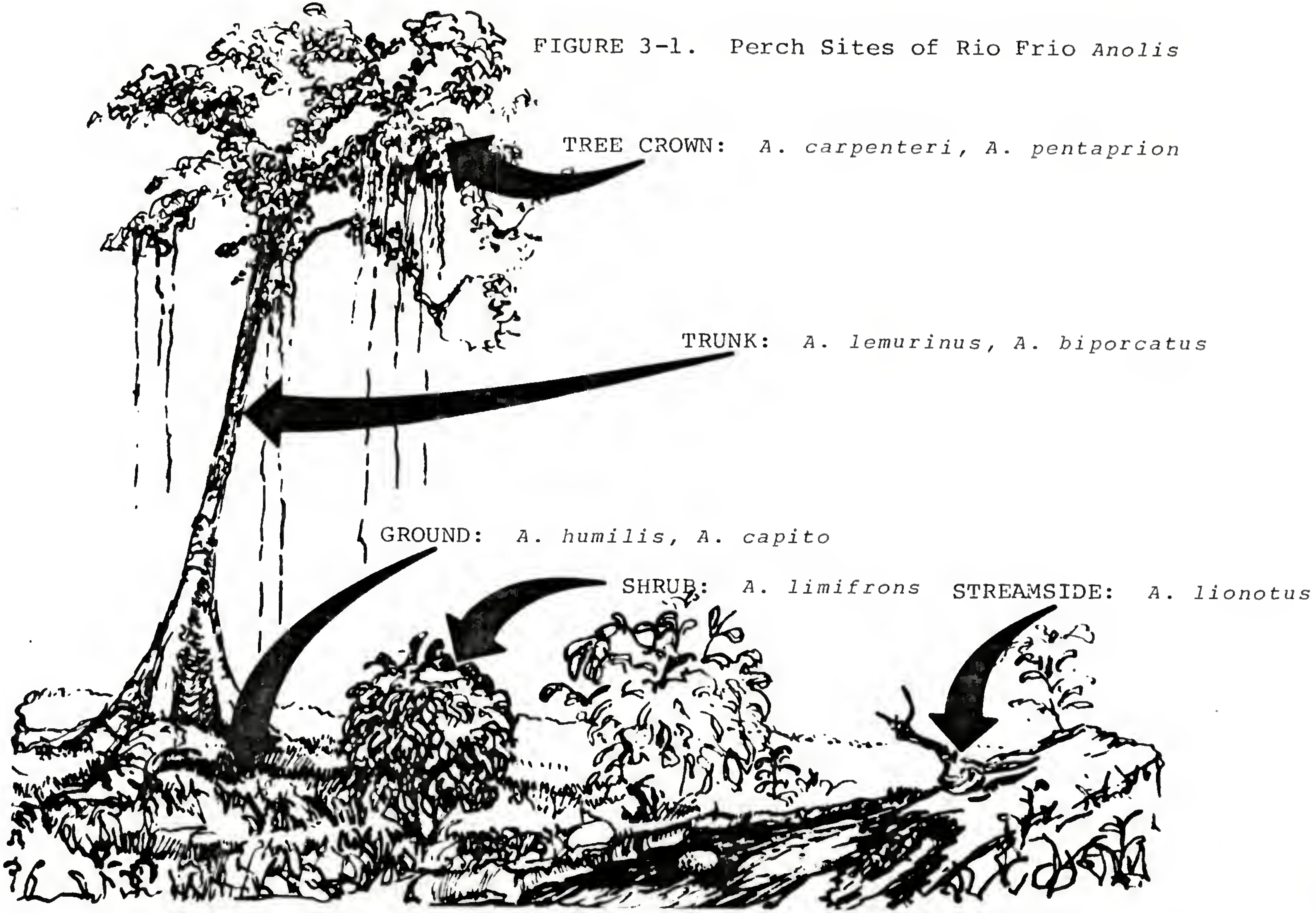


FIGURE 3-1. Perch Sites of Rio Frio *Anolis*

TREE CROWN: *A. carpenteri, A. pentaprion*
TRUNK: *A. lemurinus, A. biporcatus*
GROUND: *A. humilis, A. capito*
SHRUB: *A. limifrons*
STREAMSIDE: *A. lionotus*

IV. BODY SIZE

1. Introduction

The size of animals has always been of theoretical interest to zoologists, and Hutchinson's (1959) classic observations on size ratios of closely related species pointed the way to an interesting and fruitful area of investigation for ecologists. How do the sizes of sympatric, closely related species increase or decrease their ability to co-exist? From Hutchinson's (1959) own ratio suggestion, several authors have proposed various models, and many others have compared sizes within a variety of taxa (See Schoener, 1974, for an extensive review.). The sizes of anoles in simple and more complex West Indian faunas have been the subject of numerous studies (Schoener 1967, 1968, 1969a, 1969b, 1969c, 1970; Schoener and Gorman, 1978; Williams, 1972; and others). Only Fitch (1976) and Duellman (1978) have discussed size in sympatric mainland species.

Two particularly interesting generalizations have come from these studies. From the work of Schoener, have come what Williams (1972)called Schoener Rules:

> An anole occupying an island without congeneric competition tends to a range of sizes with maximal head lengths of between 20 and 25 mm and maximal snout-vent lengths of between 65 and 96 mm. (p. 52)

> If two anole species occur on an island, one will be smaller and the other larger, the ratio of the two sizes ranging from 1.5 to 2. (pp. 57-58)
>
> The greater the diversity of island anole faunas, the greater the disparity between the largest and smallest species. (p. 48)

These are rules meant to apply only to anoles in the West Indian islands, but they also appear to have some application to the more complex faunas of the mainland.

A second tentative generalization comes from Williams' (1972) fascinating inferential model of the historical coadaptation of the complex anole fauna of Puerto Rico. Building upon a foundation of comparative osteology, karyotypes, electrophoretic patterns and ecological information, Williams has attempted to reconstruct the probable course of evolution of the Puerto Rican anoles. From this and his wide knowledge of other anole faunas, Williams (1972) concluded that Puerto Rican anoles (and supposedly other anoles in complex island faunas)

> are first able to utilize size differences as a major means of syntopic co-existence. Beyond the stage of the third species, however, size ceases to have the same importance, and spatial shift . . . and climatic shift . . . become essential elements in the adaptations that permit the addition of species to the fauna. (pp. 87-88)

In light of these ideas, it would seem reasonable that any discussion of the ecology of anoles should first focus on size distribution among the species under consideration. That is the purpose of this section.

2. Materials and Methods

Times and places in which collections were made are described above (section II). All anoles collected at Río Frío are considered in this section. Anoles were taken during the morning and early afternoon, usually 9:00 A.M. to 2-3:00 P.M., and held in plastic bags until processing. As soon as possible after collection, usually within six hours, each lizard was weighed (alive) to the nearest 10 mg on an Ohaus balance. Each was then killed by an injection of sodium nembutal, and the snout-vent length and tail length were measured to the nearest 0.5 mm with a plastic ruler. Head and hind leg measurements (with a vernier caliper) and lamellae counts (See Appendix 1) were made after the lizard had been preserved in 10% formalin. Sex was determined by dissection (See Appendix 2).

An outstanding problem of any morphological comparison of different taxa is to determine which specimens should be compared. I considered four possibilities:

1. All specimens of each species. The weakness of this is that collecting bias might increase or decrease the mean size data.
2. Sexually mature adults. Assessment of egg production makes this method plausible for females, although seasonal cessation of reproduction is a problem in

some species. For males, however, seasonal variation in testis size and sperm production in relatively small "subadult" size males (Fitch, 1956) makes designation of a minimum adult male size extremely arbitrary.

3. The ten (or other arbitrary number) largest of each species. This would be useful if maximum size were desired, but sample size affects this choice too greatly for its use here. For example, the ten largest individuals of *A. capito* comprise 43% of my collection of that species, while the ten largest *A. limifrons* make up only 2.8% of my collection of that species.
4. The largest third (or some other fraction) of each species. This essentially eliminates the effect of sample size, yet, if the fraction is appropriately small, a reasonable sample of "largest adults" can be compared. For a more thorough discussion of this method, see Schoener (1969c).

Because an unbiased approximation of adult size is desirable for size comparisons, I have chosen the fourth alternative, carried out in the following manner. All specimens of each category considered (species, sex or collecting period) were ordered from longest to shortest. The length of the individual that was one third of the number of specimens from the longest was used as the lower limit for that sample. All specimens of that length or greater are used in size comparisons for that category, regardless of whether it is length or weight being compared. When used hereinafter, the term "longest third of" will refer to such a sample of the indicated category.

3. Sexual Dimorphism

Inasmuch as sexual dimorphism in body size is often strong in anoles (Rand, 1964, 1967a; Schoener, 1967, 1968, 1969c; Schoener and Gorman, 1968; Fitch, 1976), it was deemed appropriate to determine the pattern(s) and degree of intraspecific sexual dimorphism before making size comparisons among the species. Table 4-1 lists means and standard errors for snout-vent length (SVL), head length (HL) and body weight (BW) for all specimens of all eight species of Río Frío anoles. Table 4-2 indicates the ratios and significance of differences between those means. All eight species show a significant ($P<.05$) degree of sexual dimorphism in all three parameters except in the case of *A. biporcatus* for HL.

Two patterns of dimorphism are seen, one in which the females are larger than the males (6 species), and the second in which the males are larger than the females (2 species). The patterns and relative positions (Fig. 4-1) are fairly consistent for SVL, HL and BW. Using measurements from both living and preserved specimens, Fitch (1976) examined sexual dimorphism in 54 groups of anoles from Mexico to South America, but primarily middle America. He found SVL ratios as low as 0.80 (*Anolis vittigerus* of Panama) and as high as 1.36

(*A. cuprinus* of xeric Mexico), but only in 34 of 54 was the dimorphism significant. In his samples of *A. biporcatus*, *A. carpenteri* and *A. lemurinus*, males and females were not significantly different in SVL. Differences in our findings may be due in part to inadequate sampling of large males (*lemurinus*, *lionotus*, and *pentaprion*) by me and/or Fitch's combining of samples from various localities, seasons or years. SVL ratios in the six species studied by Duellman (1978) at Santa Cecilia, Ecuador, ranged from 0.89 (*A. trachyderma*) to 1.10 (*A. punctatus*).

The pattern in which the males are larger than the females is the rule in West Indian anoles, especially in solitary species (Schoener, 1969a). This is apparently true also for mainland Alpha anoles. Both species which have larger males than females reported by Duellman (1978) are in the Alpha section of *Anolis*. All seven of the Alpha anoles measured by Fitch (1976) have larger males (significant in 6 of 7).

In Beta anoles, both patterns are common, but seem to sort out on a climatic (faunal size?) basis. Seventeen populations studied by Fitch had significantly larger males. He considered 12 of the 17 (including *A. lionotus* and *A. pentaprion*) to be primarily inhabitants of "severely seasonal" climates. These are areas which also have reduced anole faunas, compared to lowland rain forests. Only 3 of 21 Beta groups attributed to "lowland rain forests" by Fitch have significantly larger males. Of the 11 populations having significantly larger females, eight are "lowland rain forest" forms, and the other three inhabit "montane or cloud forest" areas, both of which are "relatively aseasonal." No species which have the females larger than the males inhabits severely seasonal areas. The Río Frío anoles fit this pattern precisely.

The development of sexual differences in solitary anoles, in which males are always larger than females, is seen to be a result of lack of congeneric competition (Schoener, 1967). The two Río Frío species with larger males are the two with the least congeneric pressure. *A. lionotus* is the only anole which normally occurs in the riparian microhabitat, i.e. it is essentially a solitary anole, and it very closely fits the solitary anole size pattern. Another point, which holds for *A. lionotus* (but not for *A. pentaprion*) is Schoener's (1969b) observation that relative head size is less in solitary anoles. Table 4-3 indicates that *A. lionotus*, the "most nearly solitary" anole at Río Frío, has the shortest head relative to SVL. *A. pentaprion* inhabits the outer branches and twigs of the forest crowns. No other anole, with the possible exception of the much smaller *A. carpenteri*, overlaps with it in this exposed, climatically severe microhabitat.

The pattern in which the females are larger than the male is seen by Fitch (1976) to be an asset to species in seasonal habitats, allowing them to maximize egg/young production. While the six Río Frío species with this pattern are all primarily inhabitants of aseasonal microhabitats, these are also species which generally occur with the greater numbers of congeneric competitors and can, therefore, least support the food niche expansion that sexual dimorphism requires. Any increase in the number of anole species in a fauna will result in a general decrease in the availability of prey. Most particularly this will reduce the density of the least common large items, which are the prey of the large males in dimorphic species (Schoener, 1967, 1968; Schoener and Gorman, 1968). Schoener's (1969a, 1969b) models and examples (1969b, 1970) suggest that such an increase in food competition might result in a reduction of body size of all species, as smaller lizards are better able to exploit the more numerous small prey items. It would seem a reasonable explanation then, that the general anole pattern in which males are larger than females is abandoned in rain forest Betas because of the greater competition in multi-anole fauna. Male size is more reduced than is female size giving the size advantage to the reproductively more important, egg producing females. The following section (V) will further explore sexual differences in food.

4. Interspecies Comparisons

When an anole species exists without congeneric competitors, Schoener (1967, 1968, 1969c) suggests that an optimum size exists. When more than one species is present, sizes must diverge from the solitary anole size to alleviate pressure on particular prey sizes. Table 4-1 indicates the wide range of sizes of Río Frío *Anolis* (Fig. 4-2, 4-3). Note the range, from a minimum mean SVL of 33 mm for *A. humilis* males to a maximum of 91 mm for *A. biporcatus* females, an almost threefold difference. As would be expected, the difference in weight is even greater, from 0.65 g (*A. carpenteri* males) to 17.1 g (*A. biporcatus* females), a difference of over 26 times.

The expectation for a complex assemblage of species is that each species will differ from the next by some constant factor. Hutchinson (1959) found a range of 1.1 to 1.4 with an average difference of 1.3 times, in a variety of taxa. Table 4-4 shows that this is not the case for Río Frío anoles. Indeed, if eight species could exist with the smallest 33 mm in SVL and the length of each larger species increased by 1.3 times, the largest in the sequence would be just over 207 mm SVL, much larger than any mainland anole. To complicate this possibility further, Schoener (1970) has shown that the separation ratio should increase between larger species, so the largest in an eight species sequence would be much larger than any known anole. Since there is apparently not a constant or increasing ratio between all eight species at Río Frío, is it possible to subdivide the assemblage into some logical grouping that will show the expected pattern?

One possible sorting of species might be along phyletic lines. The species groups (or series) of Etheridge (1960) apparently represent well established evolutionary lines. Table 4-5 shows that, within each of the three series represented at Río Frío, the separation ratios are not exactly in keeping with Hutchinson's (1959) suggestion. The two members of the *chrysolepis* series are too widely separated. In the *fuscoauratus* series two species are too close, and the third is too large. Finally, in the *petersi* anoles, the females of the two smaller species are separated by too large a ratio, though the males fall in the low end of Hutchinson's bracket, and the larger two are just barely different enough to pass the lower limit. In fact, only 1 out of 10 SVL comparisons and 5 of 10 for HL fall within the 1.1 to 1.4 range, even though the average separation ratios are near 1.3 (1.32, SVL; 1.30 HL). Though a slight expansion of the ratio range would encompass most, if not all the ratios in Table 4-5, perhaps something other than a phyletic grouping might yield a more logical, consistent set of size relationships.

In an evolutionary sense, there seems to be no reason why congeners should differ in size simply because of phyletic relationship. Indeed, Hutchinson (1959) proposed that the divergence of syntopic species pairs occurs because of their ecological similarity. Therefore, ecological resemblances (microhabitat, perch site or structural niche) provide a better basis for grouping the species. Most of the anoles which I collected or observed at Río Frío were in the area of newly felled trees. With this type of data, it is not possible to establish numerical boundaries on the structural habitat of each species as is frequently done (Rand, 1964; Schoener, 1967, 1968; Schoener and Gorman, 1968; Schoener and Schoener, 1971a, 1971b; Andrews, 1971a, 1971b). However, for the discussion here, general descriptions of the habitats (such as those given in Section III) will be quite useful. As Williams (1972) explains with regard to habitat similarity in two Puerto Rican anoles:

> They both may be crudely described as crown animals of the shaded forest. It is possible to quibble a bit about this but the same modal situation describes both. A giant anole such as *cuvieri*, though it is, in fact, seen some of the time at every level (personal observation), is most often seen high in the crown. A dwarf anole such as *occultus* is seen on branches and twigs of small diameter . . . and therefore not infrequently on bushes and vines, but certainly its modal structural niche includes the crown. (p. 74)

The eight Río Frío species are best sorted into four groups:

1. Ground dwellers. This set includes *A. humilis* and *A. capito*, both of which inhabit tree bases, logs and the intervening ground surface.
2. Riparian species. Only *A. lionotus* fits here. It is thus horizontally removed from the other seven species.
3. Trunk dwellers. Included here are *A. limifrons*, primarily an inhabitant of lower trunks, smaller trees and low shrubs; *A. lemurinus*, found on larger, higher trunks; and *A. biporcatus*, on large trunks up to, and possibly into, the base of the crown.

4. Crown inhabitants. Although *A. biporcatus* might be included here, I am using this to mean only the small branches and twigs, the habitat of *A. pentaprion* and probably *A. carpenteri*.

Table 4-6 gives the length ratio of the eight species grouped by perch site.

The extension of the Schoener Rules (Williams, 1972) and other findings of Schoener (1970) to Río Frío anoles leads to the expectation that: (1) when an anole is without congeners in it's particular habitat, it will tend toward a particular, sexually dimorphic size pattern (55-75 mm SVL for males, 40-60 mm SVL for females); (2) when two anoles share a microhabitat, they will differ by a factor of 1.5 to 1, with one larger and one smaller than the solitary anole size; and (3) when three anoles occupy the same structural level, the size ratio will be greater between larger species than between smaller. Schoener (1970) found an average ratio of 1.5 between smallest and 2.2 between largest species in 10 syntopic trios. The Río Frío anoles seem to fit these expectations.

The only anole that rarely shares it's habitat with other anole species is *A. lionotus*, and it clearly fits the expected pattern, except that there is not quite as much sexual dimorphism as expected. One factor that might push the female size upward, i.e. limit the dimorphic spread, is the presence of the smaller, more numerous *A. humilis* on the adjacent, non-riparian forest floor.

Two anole habitats, the ground and the crown, are also relatively close to expectation. The two anoles with the lowest perch sites, *A. humilis* and *A. capito*, are on either end of the solitary anole size range, but they are separated by more than the 1.5 to 2.0 suggested by rule two. The exceptionally small size of *A. humilis* is perhaps explained by its partial microhabitat overlap with *A. limifrons*. This small, abundant species might compete in such a way as to push the size of *A. humilis* down. In fact, both *A. humilis* and *A. limifrons* may be reduced in size by any overlap (Schoener, 1969a, 1969b). The crown anoles, *A. carpenteri* and *A. pentaprion*, are separated by the required size range in males, but not in females -- this being due to their having opposite patterns of sexual dimorphism. Though *A. carpenteri* is below the bottom end of the solitary anole size range, *A. pentaprion* is not larger than the solitary size which rule two specifies it should be. This may be due to the small sample size. However, in equally small samples, Fitch (1976) found a mean of 74.2 mm SVL for male and 60.0 mm for female *A. pentaprion*. These measurements would make *A. pentaprion* males 2.03 times and females 1.45 times the length of *A. carpenteri* and just longer than the size range of solitary anoles. It may be that the size of *A. pentaprion* is held down by the influence of the larger *A. biporcatus* in the crown -- or even by the presence of *Polychrus gutturosus*, a larger, although primarily vegetarian iguanid which was found in crowns at Río Frío.

The only place where three species of anoles regularly perch is the area broadly termed "trunk." Here the pattern of increasing separation in larger species (Schoener, 1970) is seen, although the magnitude is somewhat less than Schoener's average for 10 islands. In both sexes, the difference in length between *A. biporcatus* and *A. lemurinus* is greater than the difference between *A. lemurinus* and *A. limifrons*.

In general then, the sizes of Río Frío anoles are well explained by Schoener's island patterns if habitat types are considered separately. That small anole faunas on West Indian islands are isolated by sea water, while the Río Frío anoles are segregated only by the much more nebulous boundaries of perch site preference, should explain the slight variation.

5. Body Weight to Length Relationships

Schoener (1969a) predicted that weight could be related to length by a power function {such as $BW=a(SVL)^b$} and that the power, b, ought to be close to 3, in groups such as *Anolis* lizards. He was able to confirm this only with data for the Puerto Rican *A. gundlachi* from Turner et al. (1965). He also expected that b might prove adaptive where there is an advantage in increased length without increased weight, as in a twig inhabiting anole. Data from Río Frío *Anolis* fit these expectations quite well (Table 4-7, Figs. 4-4 to 4-11). The exponent b ranges from 2.46 to 3.27, with a mean of 2.91.

Because of the weight increase associated with the reproductive activity of larger females, the regression line for females bends more than the curve for males. For females b averaged 2.98, while the mean for males was only 2.83. In all species except *A. lemurinus*, males have a lower b than females, reflecting the relative slimness of large males. This difference was significant only for *A. limifrons* and *A. biporcatus* (Table 4-8). Male *A. limifrons* often perch higher than females (Fitch, 1975), so the "slimness" of males may be an additional aid in moving along small stems and vines, or over leaves. No information is available on sexual differences in perch heights of *A. biporcatus*.

Though comparable reports are not available for other *Anolis*, at least two other tropical iguanids seem to show the same sexual difference. In two Costa Rican populations of *Basiliscus basiliscus*, Van Devender (1978) found males to have a significantly lower b than females. Recalculation of weight-length regression equations for *Ctenosaura similis* given in a different form by Fitch and Henderson (1977) also show a higher b for females than males.

Comparisons of b between pairs of species show few differences (Table 4-8). The exceptionally slim *A. carpenteri* have a lower b than males of all other species. This difference is significant for comparisons with all species except *A. humilis* and *A. pentaprion*. This may reflect a real adaptation to the twig-vine habitat, or it may be an artifact of the rather small, restricted sample of *A. carpenteri* since 14 of 21 weighed were within 5 mm in SVL and 12 were within 2 mm

(Fig. 4-6). Female *A. biporcatus* have a higher b than all other females, but this was significant only for comparisons with *A. carpenteri* and *A. lemurinus*. The large b may reflect the fact that *A. biporcatus* perches only on the broad trunks and large limbs of trees; but more likely it simply reflects the fact that *A. biporcatus* females are by far the largest anoles at Río Frío, and are almost always gravid.

6. Seasonal Variation in Size

There are two ways in which seasonality may cause differences in the sizes of lizards. A decrease in mean size may be caused by changes in growth rate or by different reproductive rates, which will alter the fraction of small lizards in the population. A change in the weight-length regression power, attributable to a size dependent change in food consumption, could be the cause of a seasonal difference. Even though little seasonality is apparent at Río Frío (see Section II), anoles may respond to minor variations. In this section that possibility will be considered.

Table 4-9 shows SVL, HL and BW of four species of Río Frío *Anolis* for each of the four collection periods. Samples of the other species were too small for adequate seasonal comparison. Table 4-10 shows significance of seasonal differences in SVL and BW (see also Figs. 4-12, 13, 14, 15).

A. humilis shows very little seasonal change. Females are largest (both SVL and BW) in the September sample, the climax of the rainy season, but this is significant only when compared to February, the driest season. There are no significant changes in the males of *A. humilis*.

Size of *A. limifrons* is affected by a decrease in the number of large females and an increase in the number of small males in the November sample, and by a decrease in the number of juveniles and small of both sexes in the September and May samples. The size then has an apparent "dip" at the end of the rainy season. A similar pattern was seen by Fitch (1973a) in *A. limifrons* from Turrialba, Costa Rica, which has a rainfall pattern similar to that of Río Frío. In both sexes, May specimens were the longest, but were not as heavy as the shorter September lizards. This would seem an indication that they are not feeding as well at the end of the dry season as they did during the wet months. Even though the sample sizes are very small, *A. lemurinus* and *A. lionotus* appear to be similar to *A. limifrons* in seasonal size pattern. Both have a late rainy season decrease in mean size, with an increase in length through May.

There is one immediately obvious difference in the BW-SVL regression curves (Figs. 4-16, 17, 18, 19)--that for May is well below all others. This is further evidence that, at any SVL, *A. humilis* or *A. limifrons* will weigh less in May than in any other period. The November curve is the highest in three of the four indicating that anoles are heaviest at the end of the rainy season.

The same pattern is approximately true for *A. lemurinus* and *A. lionotus*. Even though sample sizes are small for some periods and no *A. lionotus* were weighed in September, the regression curves of the rainy season samples are highest, and the May curves are lowest (Figs. 4-20, 21), as is true for *A. limifrons* and *A. humilis*. The May curves are altered somewhat by the absence of juvenile specimens of either *A. lemurinus* or *A. lionotus*.

Differences in b, the exponent of weight-length relationships are not so easily explained (Tables 4-11, 12). First, for *A. humilis* and *A. limifrons* in all periods, b is larger for females than for males as found in the preceding section for all species. This is significant only for the two rainy season samples of *A. limifrons*. But there is some variation within the sexes that is more puzzling. In three of the four species, the May samples have the highest b, although in some comparisons this difference is not significant. The regression exponent is low in most February samples and low in September samples of *A. humilis*.

The regression exponent, b, is essentially the factor determining that the big get bigger, i.e., the upward curvature of the regression line. As such, it appears that even though most groups are lightest in May, the longer individuals are comparatively heavier than the shorter ones, an indication that a late dry season food decline has a more pronounced effect on smaller lizards. This may be caused by a variety of factors, probably including actual physical struggle for food items, size proportional territory (and, therefore, more potential prey for larger individuals), and higher perches and a larger scanning radius for larger anoles. The only exception is *A. lemurinus*—the sample of May females has a heavier BW as well as a longer SVL. However this is from a sample of two, so the differences are not significant.

The only exception to the May peak of b is the case of *A. lionotus*. In *A. lionotus*, the complete absence of small individuals causes the regression line to rotate clockwise. If the curve were drawn below the SVL of the smallest May *A. lionotus* collected (56.5 mm), it would predict improbably heavy juveniles (dotted line on Fig. 4-21). If normal-sized juveniles had been collected, they might well have bent the regression curve to the "normal" pattern.

TABLE 4-1. Sizes of Longest Third of Río Frío *Anolis*

SPECIES	SEX	N_L[†]	SVL[ϕ] (mm)	HL (mm)	N_W	BW (g)
humilis	♂	53	33.22(±0.14)	9.00(±0.06)	47	0.90(±0.02)
	♀	49	35.76(±0.21)	9.51(±0.05)	44	1.23(±0.03)
limifrons	♂	72	37.15(±0.13)	9.66(±0.04)	59	0.84(±0.01)
	♀	72	39.59(±0.15)	9.94(±0.05)	60	1.09(±0.02)
carpenteri	♂	11	36.50(±0.41)	9.26(±0.17)	9	0.65(±0.03)
	♀	7	41.50(±0.42)	10.07(±0.15)	6	1.08(±0.03)
lemurinus	♂	24	47.79(±0.31)	12.39(±0.11)	18	2.28(±0.06)
	♀	13	57.38(±0.47)	14.57(±0.19)	9	4.14(±0.16)
pentaprion	♂	4	61.50(±1.86)	16.38(±0.50)	3	4.00(±0.14)
	♀	5	56.80(±0.37)	14.32(±0.19)	5	3.19(±0.04)
lionotus	♂	14	65.11(±1.20)	15.51(±0.28)	14	4.95(±0.26)
	♀	12	58.58(±0.58)	13.86(±0.14)	12	3.92(±0.11)
capito	♂	5	75.80(±1.10)	18.52(±0.10)	3	9.16(±0.77)
	♀	4	83.25(±1.25)	21.20(±0.34)	4	12.47(±0.23)
biporcatus	♂	12	88.75(±0.32)	23.45(±0.11)	10	14.54(±0.19)
	♀	8	90.63(±0.80)	23.91(±0.19)	7	17.14(±0.77)

[†] Approximately 1/3 of all those in each category - includes the longest third plus any others of the same SVL as shortest specimen in longest third. N_W (BW) may be less than N_L (SVL and HL) if not all of the longest third were weighed.

[ϕ] Given as: mean(±standard error).

TABLE 4-2.
Significance of Sexual Size Differences in Río Frío *Anolis*

SPECIES	SERIES[†]	SVL RATIO[Φ]	SIG[∇]	HL RATIO	SIG	BW RATIO	SIG
1. Females larger than males:							
lemurinus	c	0.83:1	***	0.85:1	***	0.55:1	***
carpenteri	f	0.88:1	***	0.92:1	**	0.60:1	***
capito	p	0.91:1	**	0.87:1	***	0.73:1	**
humilis	c	0.93:1	***	0.95:1	***	0.73:1	***
limifrons	f	0.94:1	***	0.97:1	***	0.77:1	***
biporcatus	p	0.98:1	*	0.98:1	n.s.	0.86:1	**
pentaprion	p	1.08:1	*	1.14:1	**	1.26:1	**
lionotus	f	1.11:1	***	1.12:1	***	1.26:1	**

[†] Series: c, *chrysolepis*; f, *fuscoauratus*; p, *petersi*.

[Φ] Ratios are mean of longest third of male:mean of longest third of female.

[∇] Significant (t test) in difference in male-female means: n.s., not significant; *, P<.05; **, P<.01; ***, P<.001.

TABLE 4-3. Relative Head Length

SPECIES	RELATIVE HL[Σ]	
	MALE	FEMALE
lionotus	0.238	0.237
capito	0.244	0.255
carpenteri	0.254	0.243
lemurinus	0.259	0.254
limifrons	0.260	0.251
biporcatus	0.264	0.264
pentaprion	0.266	0.252
humilis	0.271	0.266

[Σ] Mean HL ÷ mean SVL.

TABLE 4-4. SVL Ratios Between Species

SPECIES	SVL (mm)	RATIO[†]	SIG[Φ]
1. Males:			
humilis	33.22		
carpenteri	36.50	1.10:1	***
limifrons	37.15	1.02:1	n.s.
lemurinus	47.79	1.29:1	***
pentaprion	61.50	1.29:1	***
lionotus	65.11	1.06:1	n.s.
capito	75.80	1.16:1	***
biporcatus	88.75	1.17:1	***
2. Females:			
humilis	35.76		
limifrons	39.59	1.11:1	***
carpenteri	41.50	1.05:1	***
pentaprion	56.80	1.37:1	***
lemurinus	57.38	1.01:1	n.s.
lionotus	58.83	1.03:1	n.s.
capito	83.25	1.42:1	***
biporcatus	90.63	1.09:1	***

[†] Longer SVL ÷ shorter SVL.

[Φ] t test, comparing each with next longer; significance as in Table 4-2.

TABLE 4-5. Length Ratios by Taxonomic Series

SERIES	SPECIES	SVL (mm)	RATIO	HL (mm)	RATIO
	1. Males:				
chrysolepis	*humilis*	33.22		9.00	
	lemurinus	47.79	1.44	12.39	1.38
fuscoauratus	*carpenteri*	36.50		9.26	
	limifrons	37.15	1.02	9.66	1.04
	lionotus	65.11	1.75	15.51	1.61
petersi	*pentaprion*	61.50		16.38	
	capito	75.80	1.23	18.52	1.13
	biporcatus	88.75	1.17	23.45	1.27
	2. Females:				
chrysolepis	*humilis*	35.76		9.51	
	lemurinus	57.38	1.60	14.57	1.53
fuscoauratus	*limifrons*	39.59		9.73	
	carpenteri	41.50	1.05	10.07	1.03
	lionotus	58.83	1.42	13.86	1.38
petersi	*pentaprion*	56.80		14.32	
	capito	83.25	1.47	21.20	1.48
	biporcatus	90.63	1.09	23.91	1.13

TABLE 4-6. Length Ratios by Perch Site

PERCH SITE	SPECIES	SVL (mm)	RATIO	HL (mm)	RATIO
	1. Males				
streamside	*lionotus*	65.11		15.51	
ground and streamside	*humilis*	33.22		9.00	
	lionotus	65.11	1.96	15.51	1.72
	capito	75.80	1.16	18.52	1.19
ground	*humilis*	33.22		9.00	
	capito	75.80	2.28	18.52	2.06
trunk	*limifrons*	37.15		9.66	
	lemurinus	47.79	1.29	12.39	1.28
	biporcatus	88.75	1.86	23.45	1.89
crown	*carpenteri*	36.50		9.26	
	pentaprion	61.50	1.68	16.38	1.77
	biporcatus	88.75	1.44	23.45	1.43
	2. Females				
streamside	*lionotus*	58.83		13.86	
ground and streamside	*humilis*	35.76		9.51	
	lionotus	58.83	1.65	13.86	1.46
	capito	83.25	1.42	21.20	1.53
ground	*humilis*	35.76		9.51	
	capito	83.25	2.33	21.20	2.23
trunk	*limifrons*	39.59		9.73	
	lemurinus	57.38	1.45	14.57	1.50
	biporcatus	90.63	1.58	23.91	1.64
crown	*carpenteri*	41.50		10.07	
	pentaprion	56.80	1.37	14.32	1.42
	biporcatus	90.63	1.60	23.91	1.67

TABLE 4-7. Weight to Length Relationships

SPECIES	SEX	a	b	r
A. humilis	♂+juv.[†]	$4.66x10^{-5}$	2.82	0.981
	♀+juv.	$3.16x10^{-5}$	2.95	0.985
A. limifrons	♂+juv.	$2.84x10^{-5}$	2.85	0.975
	♀+juv.	$1.78x10^{-5}$	2.99	0.981
A. carpenteri	♂	$9.34x^{-5}$	2.46	0.981
	♀	$3.08x10^{-5}$	2.81	0.983
A. lemurinus	♂	$3.10x10^{-5}$	2.90	0.988
	♀	$4.43x10^{-5}$	2.82	0.992
A. pentaprion	♂	$2.46x10^{-5}$	2.93	0.991
	♀	$1.76x10^{-5}$	3.00	0.977
A. lionotus	♂	$2.93x10^{-5}$	2.89	0.995
	♀	$2.07x10^{-5}$	2.99	0.995
A. capito	♂	$4.12x10^{-5}$	2.84	0.993
	♀	$1.79x10^{-5}$	3.04	0.996
A. biporcatus	♂	$2.61x10^{-5}$	2.95	0.994
	♀	$0.68x10^{-5}$	3.27	0.986

NOTE: Regressions are in the form of $\ln(BW)=\ln(a)+b\ln(SVL)$ or $BW=aSVL^{b}$.

[†] For *A. humilis* and *A. limifrons* small unsexed specimens were used with both sexes.

TABLE 4-8. F Test for Difference in b

	A. humilis	*A. limifrons*	*A. carpenteri*	*A. lemurinus*	*A. pentaprion*	*A. lionotus*	*A. capito*	*A. biporcatus*	male vs. female
A. humilis		0.52	0.28	1.14	0.03	0.11	0.29	1.37	3.52
A. limifrons	0.19		0.61	2.56	0.00	0.01	0.08	1.23	4.12**
A. carpenteri	2.97	4.48*†		0.01	0.53	1.60	1.52	5.10*	3.55
A. lemurinus	0.61	0.27	10.34**		0.67	3.55	3.22	6.82*	0.73
A. pentaprion	0.06	0.04	3.95	0.01		0.01	0.02	1.17	0.04
A. lionotus	0.50	0.16	10.78**	0.04	0.03		0.27	4.03	1.66
A. capito	0.01	0.00	4.98*	0.14	0.17	0.08		1.78	1.18
A. biporcatus	0.73	0.54	16.62**	0.25	0.01	0.52	0.74		4.86*

NOTE: Upper right triangle represents o vs. o tests; lower left is o vs. o; far right column is o vs. o.

NOTE: Degrees of freedom are 1, $N_1 + N_2 - 4$

†*, $P_{(b_1=b_2)} < .05$; **$P_{(b_1=b_2)} < .01$

TABLE 4-9.
Sizes of Anoles by Collection Period

PERIOD	N_L[†]	SVL (mm)	HL (mm)	N_W	BW (g)
A. humilis ♂♂					
SEP	11	33.09(±0.30)	9.14(±0.15)	7	0.87(±0.03)
NOV	15	33.17(±o.31)	9.11(±0.10)	14	0.99(±0.03)
FEB	9	33.39(±0.47)	9.12(±0.09)	8	0.96(±0.04)
MAY	13	33.54(±0.22)	8.79(±0.11)	13	0.82(±0.03)
A. humilis ♀♀					
SEP	12	36.42(±0.48)	9.58(±0.07)	8	1.34(±0.07)
NOV	12	35.92(±0.53)	9.58(±0.13)	12	1.29(±0.05)
FEB	15	35.07(±0.35)	9.44(±0.08)	15	1.19(±0.04)
MAY	9	35.78(±0.26)	9.44(±0.12)	9	1.15(±0.06)
A. limifrons ♂♂					
SEP	16	37.00(±0.30)	9.73(±0.08)	6	0.89(±0.04)
NOV	18	36.33(±0.19)	9.55(±0.08)	17	0.83(±0.02)
FEB	12	37.21(±0.13)	9.73(±0.07)	11	0.89(±0.03)
MAY	21	38.00(±0.27)	9.69(±0.07)	21	0.84(±0.02)
A. limifrons ♀♀					
SEP	16	40.13(±0.21)	10.15(±0.09)	9	1.27(±0.04)
NOV	9	37.61(±0.35)	9.71(±0.09)	7	1.08(±0.03)
FEB	21	39.26(±0.30)	9.89(±0.11)	20	1.05(±0.03)
MAY	17	40.82(±0.18)	10.08(±0.06)	17	1.11(±0.03)
A. lemurinus ♂♂					
SEP	8	47.25(±0.76)	12.34(±0.19)	5	2.30(±0.11)
NOV	7	44.86(±2.17)	11.84(±0.44)	7	2.13(±0.25)
FEB	4	47.00(±0.58)	12.18(±0.17)	4	2.22(±0.06)
MAY	2	48.25(±0.25)	-----	2	1.95(±0.05)
A. lemurinus ♀♀					
SEP	3	59.17(±0.60)	15.10(±0.40)	2	4.73(±0.33)
NOV	3	49.17(±4.18)	13.23(±0.98)	3	2.71(±0.54)
FEB	3	53.67(±2.17)	14.10(±0.49)	3	3.35(±0.50)
MAY	2	58.75(±1.25)	14.55(±0.75)	2	4.02(±0.48)
A. lionotus ♂♂					
SEP	1	57.0	14.3	0	
NOV	4	55.13(±3.85)	13.00(±0.90)[Φ]	4	3.34(±0.63)
FEB	8	65.00(±1.53)	15.58(±0.34)	8	4.94(±0.39)
MAY	2	70.75(±2.25)	16.90(±0.40)	2	5.85(±0.44)
A. lionotus ♀♀					
SEP	0			0	
NOV	5	51.60(±2.06)	12.15(±0.05)	5	2.78(±0.38)
FEB	8	58.69(±0.56)	13.99(±0.16)	8	4.03(±0.12)
MAY	1	62.5	14.3	1	4.26

[†] Arrangement as in Table 4-1.

[Φ] N=2; head length not measured on all *A. lionotus*.

TABLE 4-10.
Significance of Seasonal Differences Size in Río Frío *Anolis*

A. humilis		SEP	NOV	FEB	MAY
mean SVL	SEP		n.s.	*	n.s.
	NOV	n.s.		n.s.	n.s.
	FEB	n.s.	n.s.		n.s.
	MAY	n.s.	n.s.	n.s.	
mean BW	SEP		n.s.	n.s.	n.s.
	NOV	*		n.s.	n.s.
	FEB	n.s.	n.s.		n.s.
	MAY	n.s.	***	*	
A. limifrons					
mean SVL	SEP		***	*	*
	NOV	n.s.		**	***
	FEB	n.s.	***		***
	MAY	*	***	*	
mean BW	SEP		**	***	**
	NOV	n.s.		n.s.	n.s.
	FEB	n.s.	n.s.		n.s.
	MAY	n.s.	n.s.	n.s.	
A. lemurinus					
mean SVL	SEP		n.s.	n.s.	n.s.
	NOV	n.s.		n.s.	n.s.
	FEB	n.s.	n.s.		n.s.
	MAY	n.s.	n.s.	n.s.	
mean BW	SEP		*	n.s.	n.s.
	NOV	n.s.		n.s.	n.s.
	FEB	n.s.	n.s.		n.s.
	MAY	*	n.s.	*	
A. lionotus					
mean SVL	NOV			**	
	FEB		*		
	MAY		*	n.s.	
mean BW	NOV			**	
	FEB		n.s.		
	MAY		*	n.s.	

NOTE 1: t-test; significance as in Table 4-2.

NOTE 2: Female comparisons are on the upper right, males on the lower left

TABLE 4-11.
Seasonal Weight to Length Relationships

SPECIES	SEX	PERIOD	a	b	r
A. humilis	♂+j	SEP	$8.07x10^{-5}$	2.66	0.979
		NOV	$2.54x10^{-5}$	3.03	0.985
		FEB	$3.79x10^{-5}$	2.89	0.996
		MAY	$1.95x10^{-5}$	3.04	0.988
	♀+j	SEP	$5.56x10^{-5}$	2.79	0.985
		NOV	$2.23x10^{-5}$	3.07	0.989
		FEB	$3.19x10^{-5}$	2.96	0.993
		MAY	$1.14x10^{-5}$	3.21	0.993
A. limifrons	♂+j	SEP	$4.11x10^{-5}$	2.76	0.990
		NOV	$4.30x10^{-5}$	2.75	0.989
		FEB	$4.33x10^{-5}$	2.75	0.985
		MAY	$0.93x10^{-5}$	3.14	0.985
	♀+j	SEP	$1.77x10^{-5}$	3.02	0.995
		NOV	$1.56x10^{-5}$	3.06	0.991
		FEB	$3.58x10^{-5}$	2.80	0.986
		MAY	$0.78x10^{-5}$	3.20	0.986
A. lemurinus	both	SEP	$1.96x10^{-5}$	3.04	0.988
		NOV	$2.87x10^{-5}$	2.94	0.995
		FEB	$5.04x10^{-5}$	2.78	0.990
		MAY	$0.39x10^{-5}$	3.42	0.958
A. lionotus	both	NOV	$2.02x10^{-5}$	2.99	0.995
		FEB	$2.36x10^{-5}$	2.95	0.994
		MAY	$20.38x10^{-5}$	2.41	0.968

NOTE: Regressions as in Table 4-7.

TABLE 4-12.
F Test for Seasonal Difference in b

A. humilis	SEP	NOV	FEB	MAY	OVSO
SEP		5.38*	1.84	9.99**	0.74
NOV	8.28**		1.09	1.61	0.15
FEB	2.76	1.10		7.84**	0.49
MAY	6.73*	0.01	1.78		2.40
A. limifrons					
SEP		0.15	3.50	2.19	5.46*
NOV	0.00		4.65*	1.22	8.80**
FEB	0.01	0.00		15.39**	0.29
MAY	9.01**	12.89**	13.38**		0.37
A. lemurinus					
SEP					
NOV	0.77				
FEB	3.12	2.24			
MAY	1.45	4.11*	6.14*		
A. lionotus					
NOV					
FEB		0.13			
MAY		6.11*	2.18		

NOTE: Significance and arrangement as in Table 4-8.

FIGURE 4-1. Sexual Dimorphism in Río Frío *Anolis*. Male:female ratios for body weight (BW), head length (HL) and snout-vent length (SVL) for Río Frío anoles and SVL for specimens measured by Fitch (1976). Bar below symbol indicates male-female difference is not significant. Symbols represent:

A. biporcatus, solid triangle;
A. capito, hollow triangle;
A. carpenteri, x;
A. humilis, hollow square;
A. lemurinus, solid square;
A. limifrons, hollow circle;
A. lionotus, solid circle; and
A. pentaprion, hollow diamond.

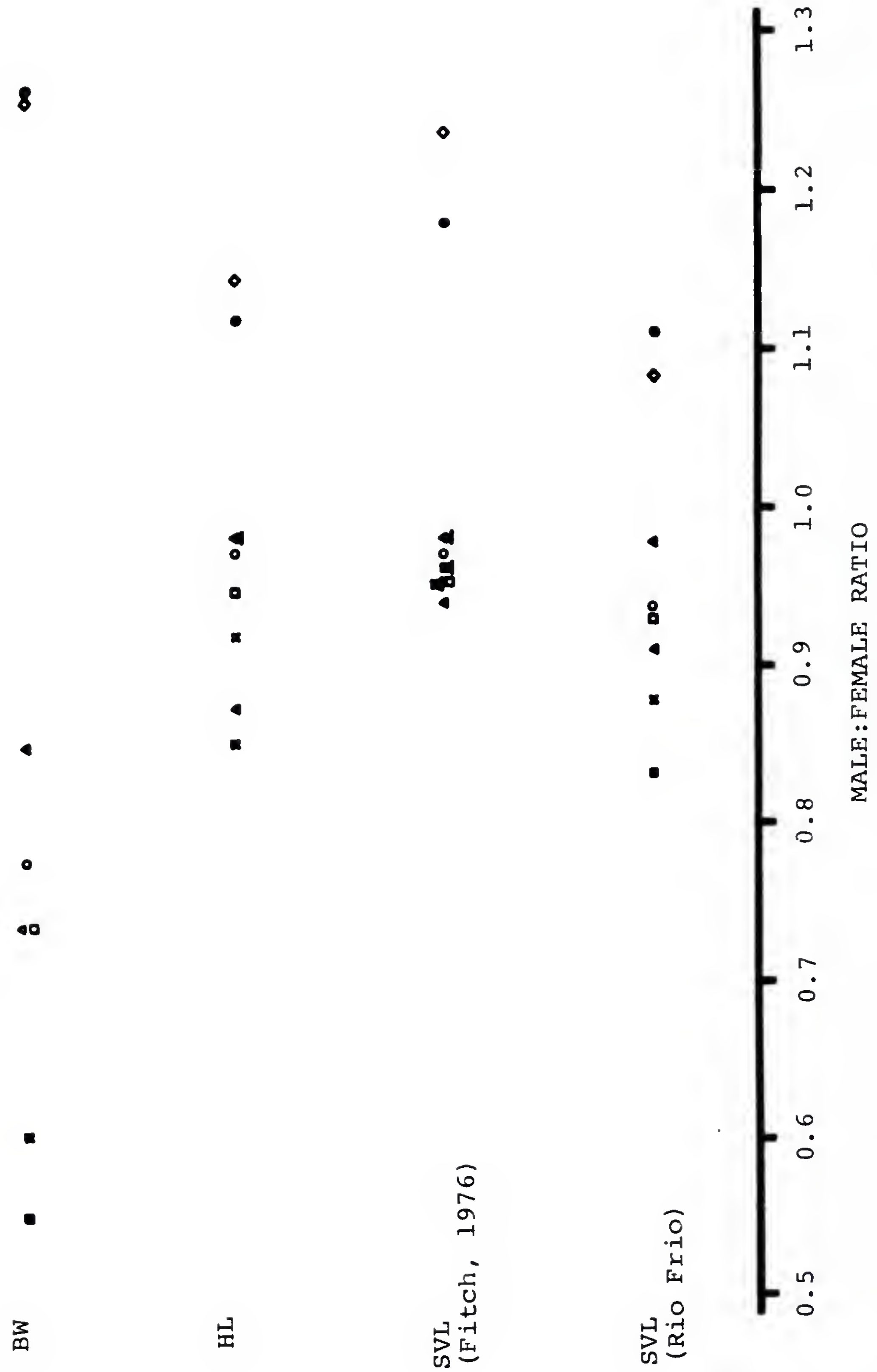

BW
HL
SVL (Fitch, 1976)
SVL (Rio Frio)
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
MALE:FEMALE RATIO

FIGURE 4-2. Snout-Vent Lengths of Longest Third of Río Frío *Anolis*. Mean SVL indicated by a horizontal line, range by a vertical line, 95% confidence interval by stippled bar (males, on right) or cross-hatched bar (females, on left), and sample size by number above each figure.

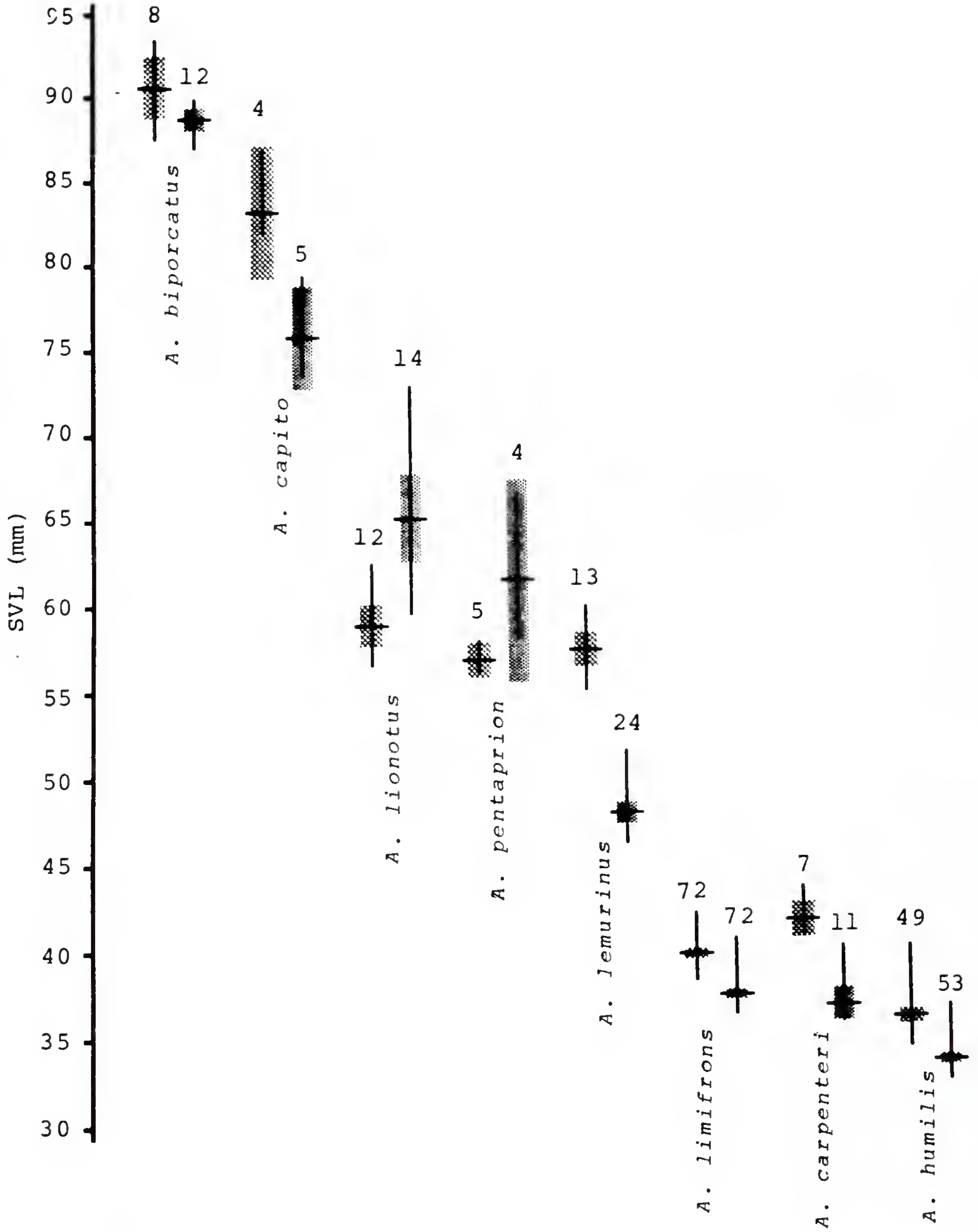

SVL (mm)
95
90
85
80
75
70
65
60
55
50
45
40
35
30
8
12
4
5
14
12
4
5
13
24
72
72
7
11
49
53
A. biporcatus
A. capito
A. lionotus
A. pentaprion
A. lemurinus
A. limifrons
A. carpenteri
A. humilis

FIGURE 4-3. Body Weight of Longest Third of Río Frío *Anolis* Mean BW indicated by a horizontal line, range by a vertical line, 95% confidence interval by stippled bar (males, on right) or cross-hatched bar (females, on left), and sample size by number above each figure.

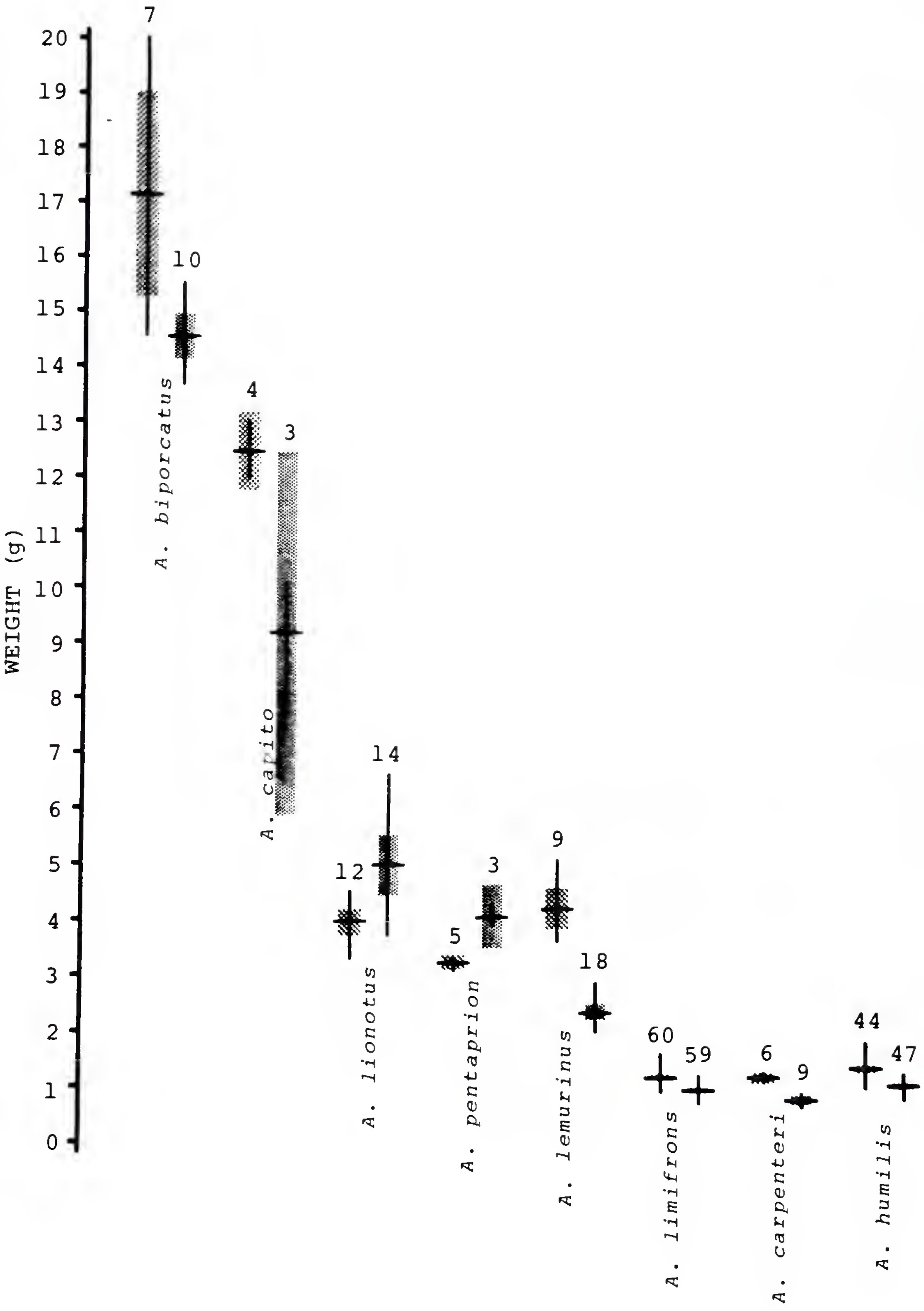

WEIGHT (g)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
7
10
A. biporcatus
4
3
A. capito
12
14
A. lionotus
5
3
A. pentaprion
9
18
A. lemurinus
60
59
A. limifrons
6
9
A. carpenteri
44
47
A. humilis

FIGURE 4-4. Weight Versus Length for *Anolis humilis*. Males are indicated by solid circles; females by hollow circles; unsexed juveniles by crosses. Curves (solid line, males and juveniles; dashed line, females and juveniles)

$$BW=aSVL^{b}.$$

Coefficients are given in table 4-7.

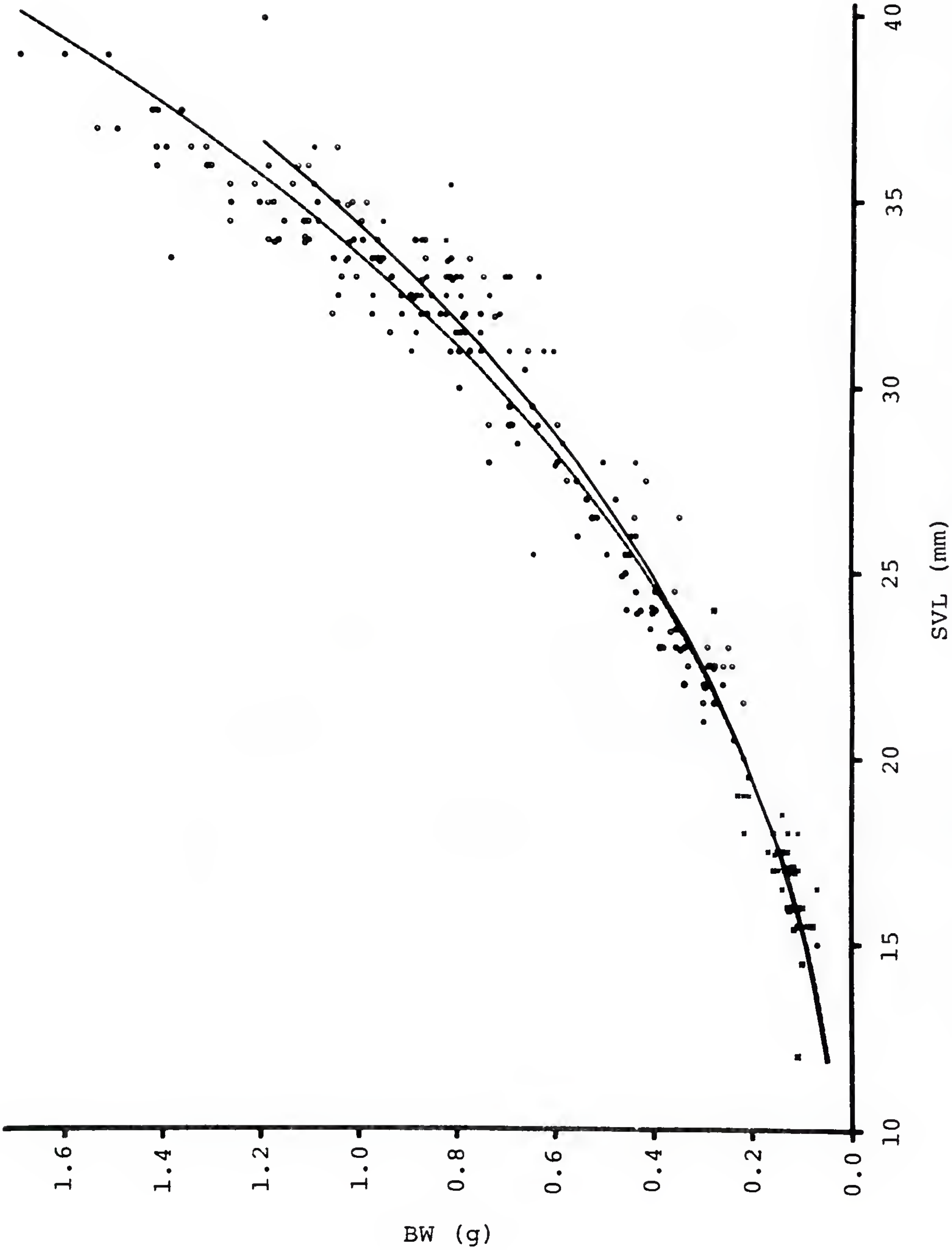

BW (g)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
SVL (mm)
10
15
20
25
30
35
40

FIGURE 4-5. Weight Versus Length for *Anolis limifrons*. Symbols as in figure 4-4.

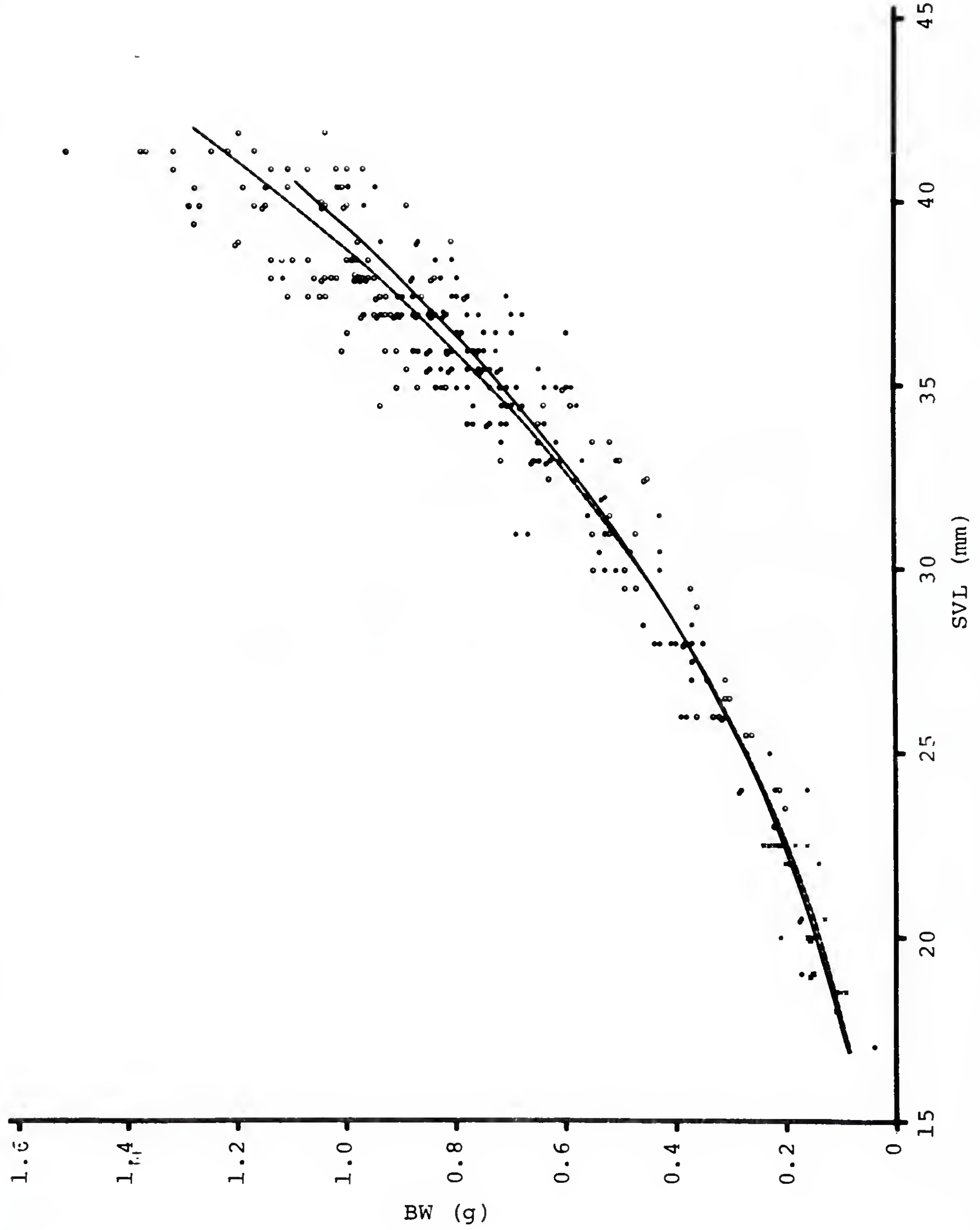

BW (g)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
SVL (mm)
15
20
25
30
35
40
45

FIGURE 4-6. Weight Versus Length for *Anolis carpenteri*. Symbols as in figure 4-4.

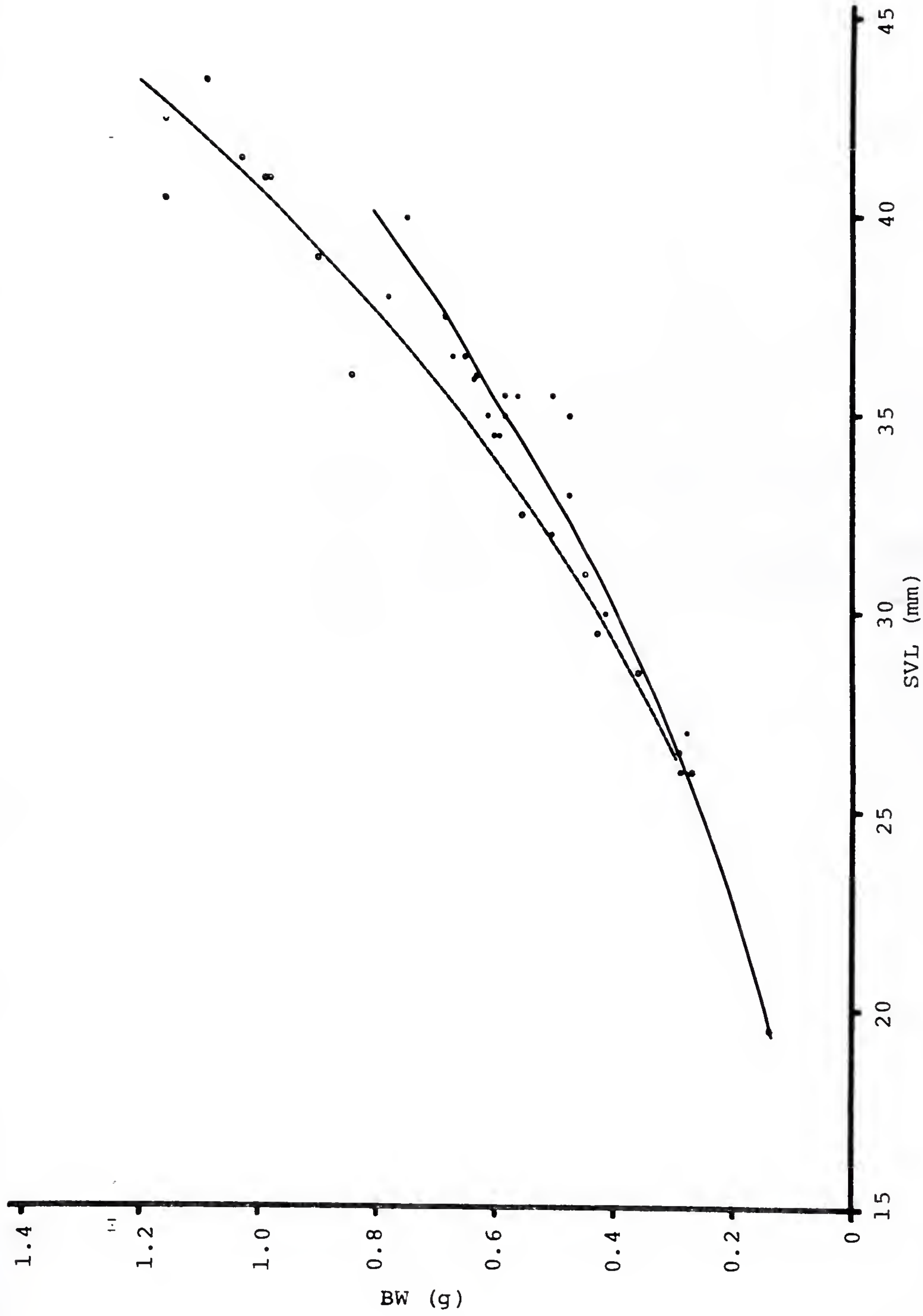

BW (g)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
15
20
25
30
35
40
45
SVL (mm)

FIGURE 4-7. Weight Versus Length for *Anolis lemurinus*. Symbols as in figure 4-4.

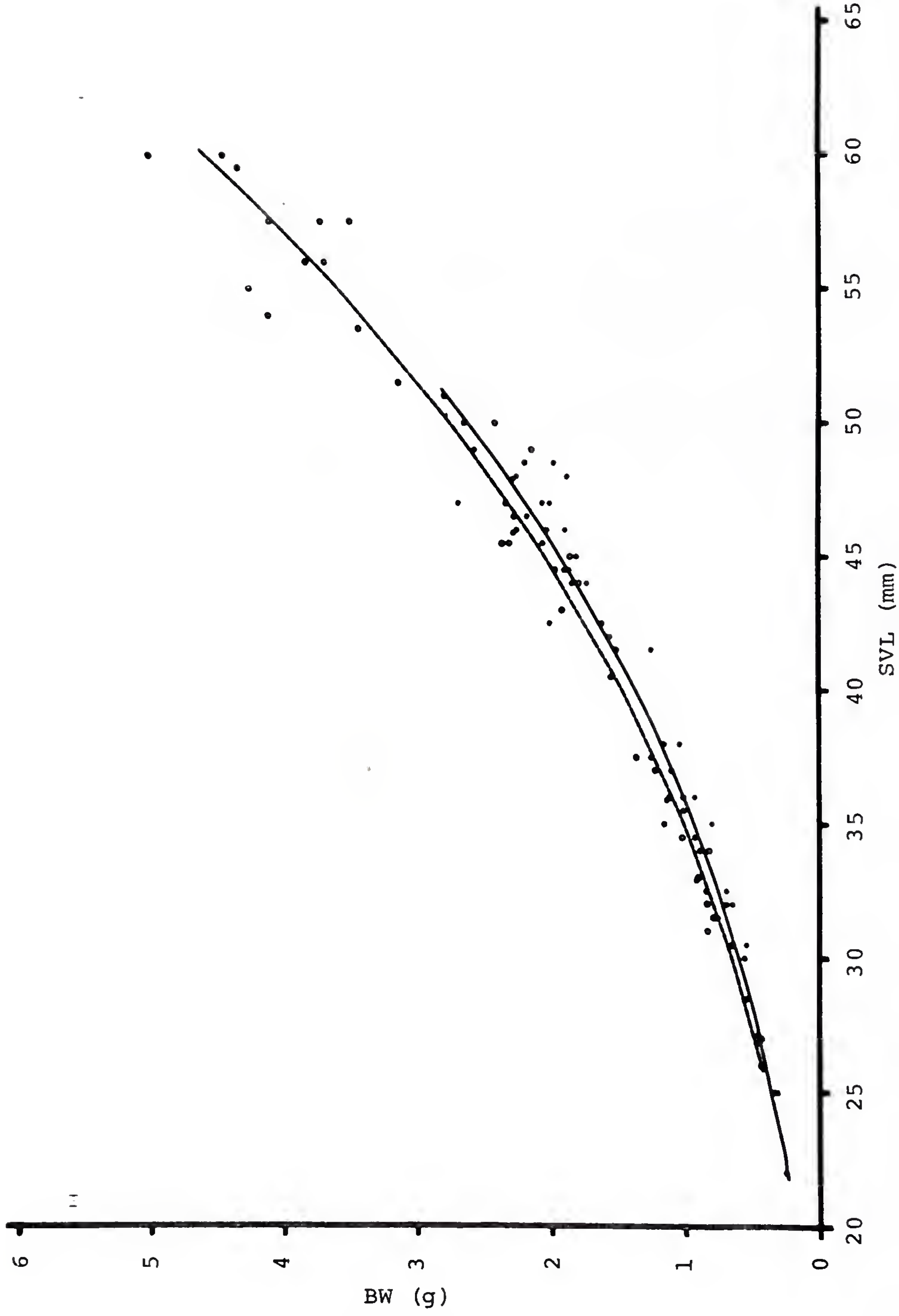

BW (g)
0
1
2
3
4
5
6
SVL (mm)
20
25
30
35
40
45
50
55
60
65

FIGURE 4-8. Weight Versus Length for *Anolis pentaprion*. Symbols as in figure 4-4.

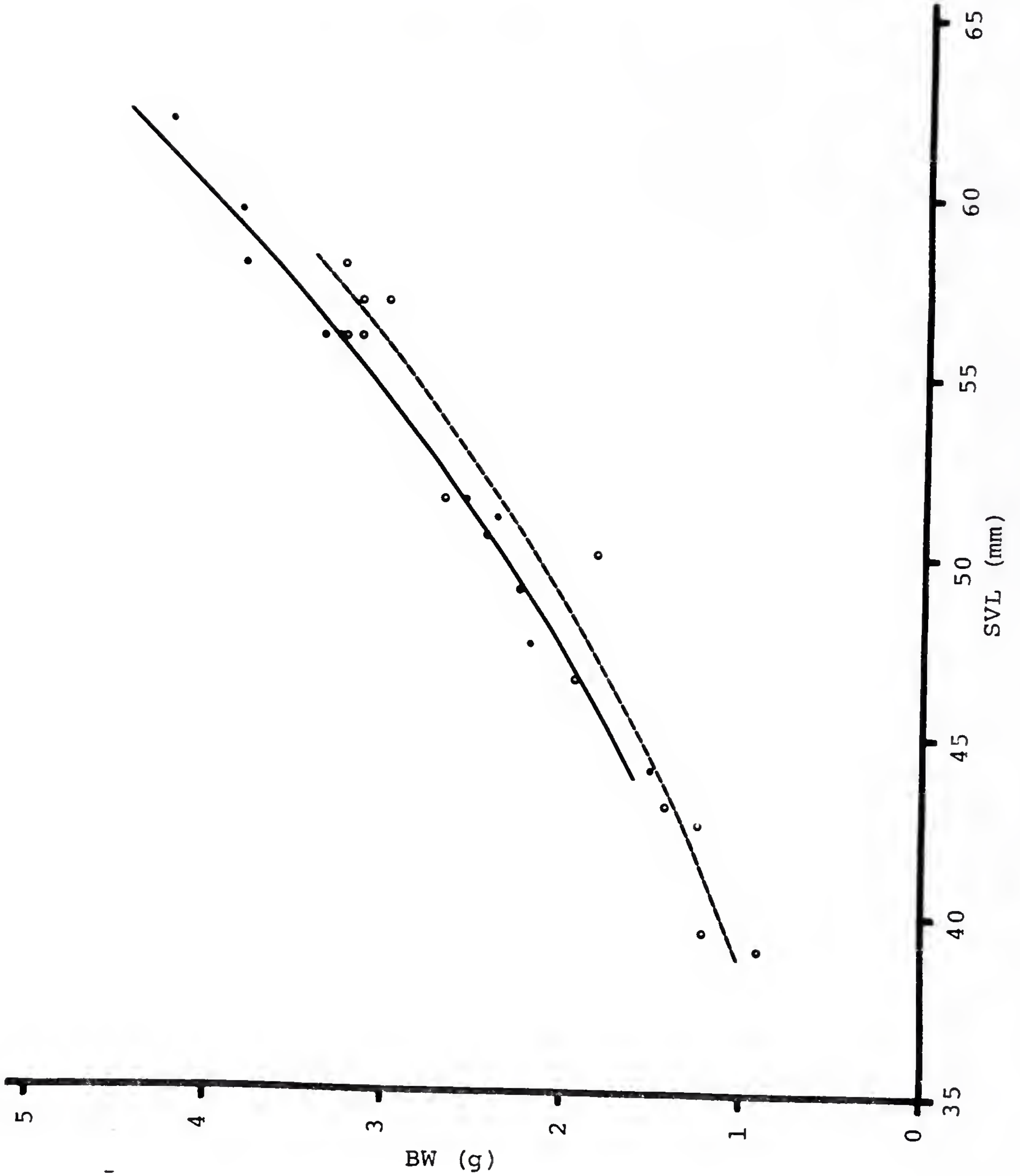

BW (g)
0
1
2
3
4
5
SVL (mm)
35
40
45
50
55
60
65

FIGURE 4-9. Weight Versus Length for *Anolis lionotus*. Symbols as in figure 4-4.

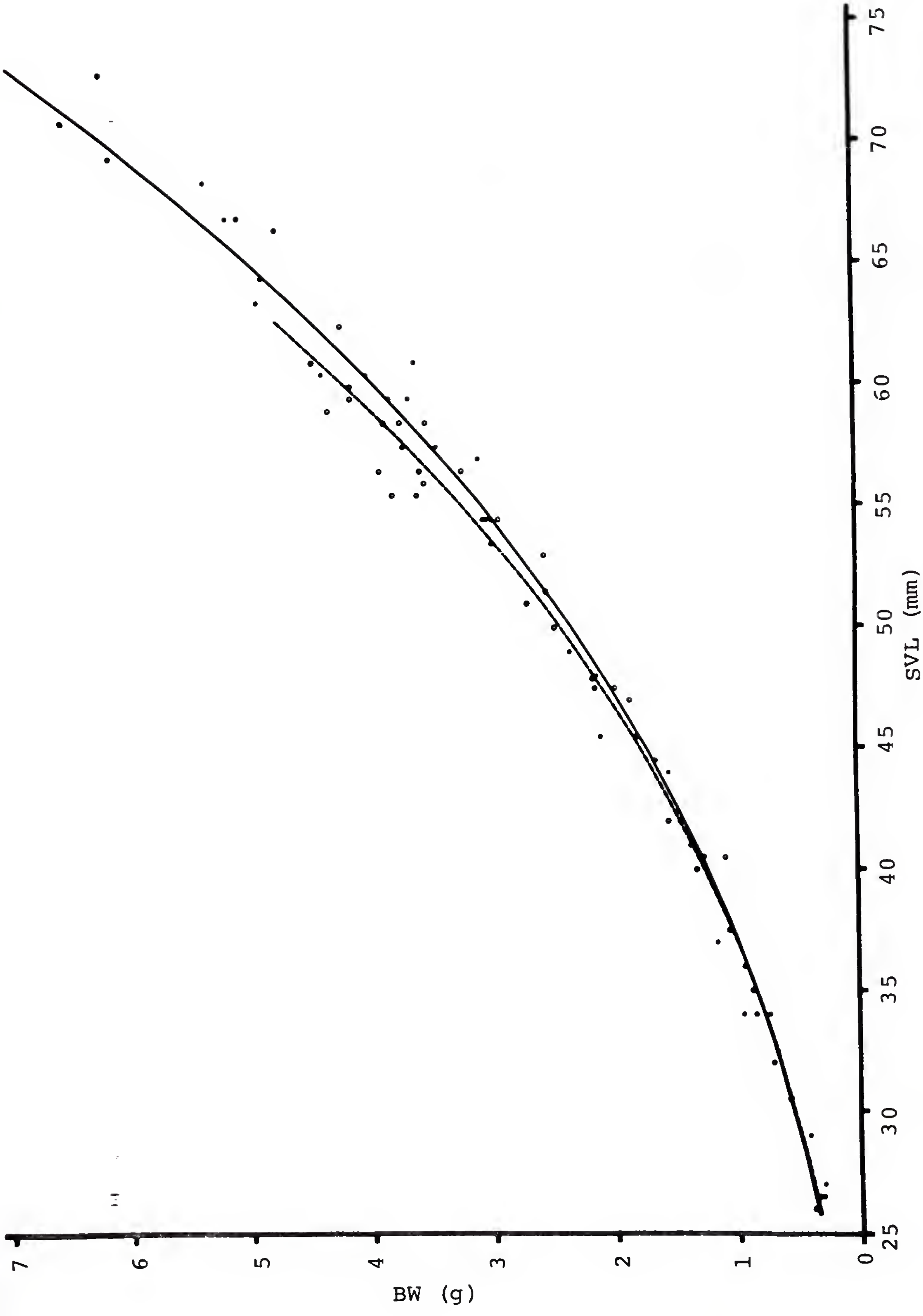

BW (g)
0
1
2
3
4
5
6
7
SVL (mm)
25
30
35
40
45
50
55
60
65
70
75

FIGURE 4-10. Weight Versus Length for *Anolis capito*. Symbols as in figure 4-4.

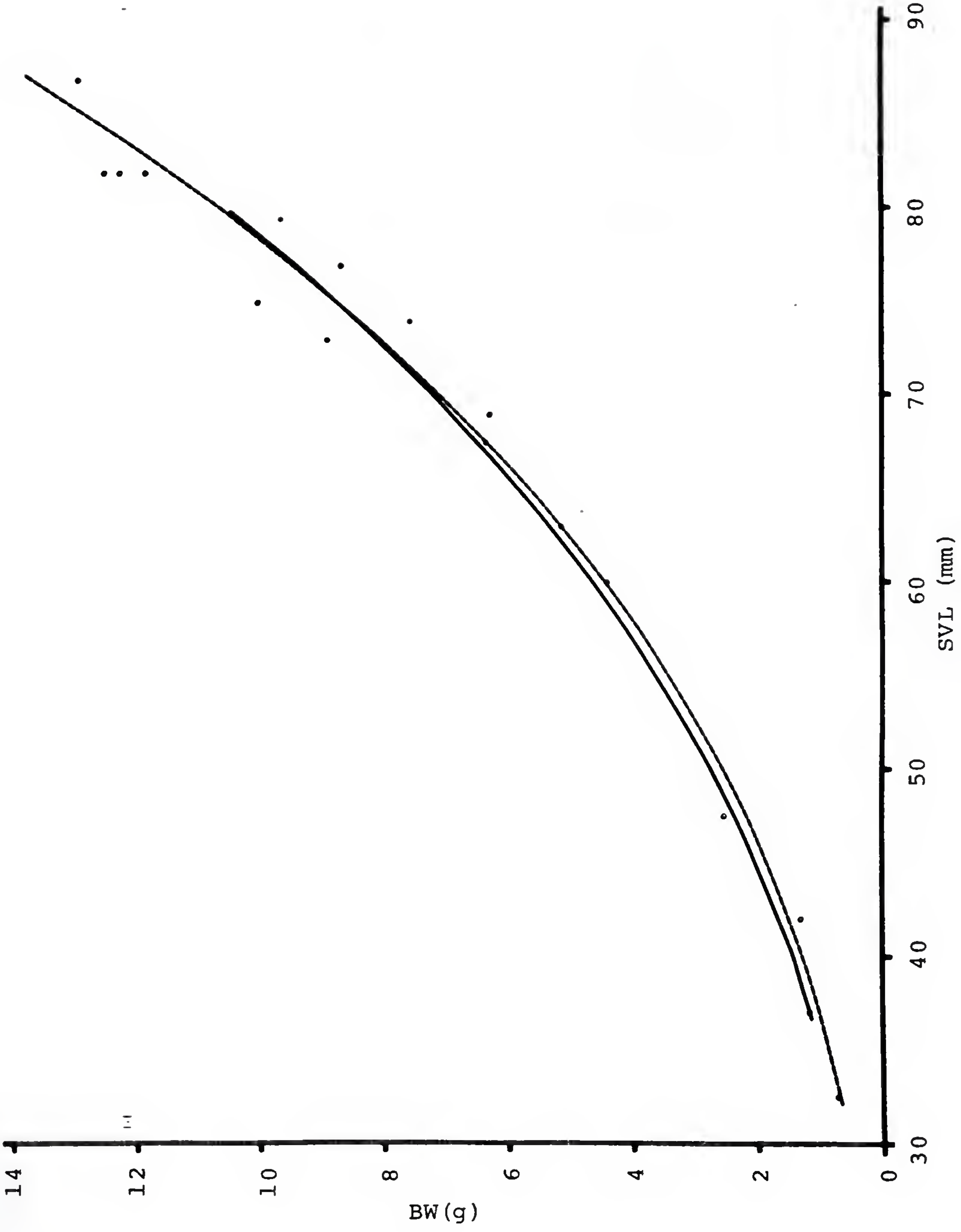

BW(g)
0
2
4
6
8
10
12
14
SVL (mm)
30
40
50
60
70
80
90

FIGURE 4-11. Weight Versus Length for *Anolis biporcatus*. Symbols as in figure 4-4.

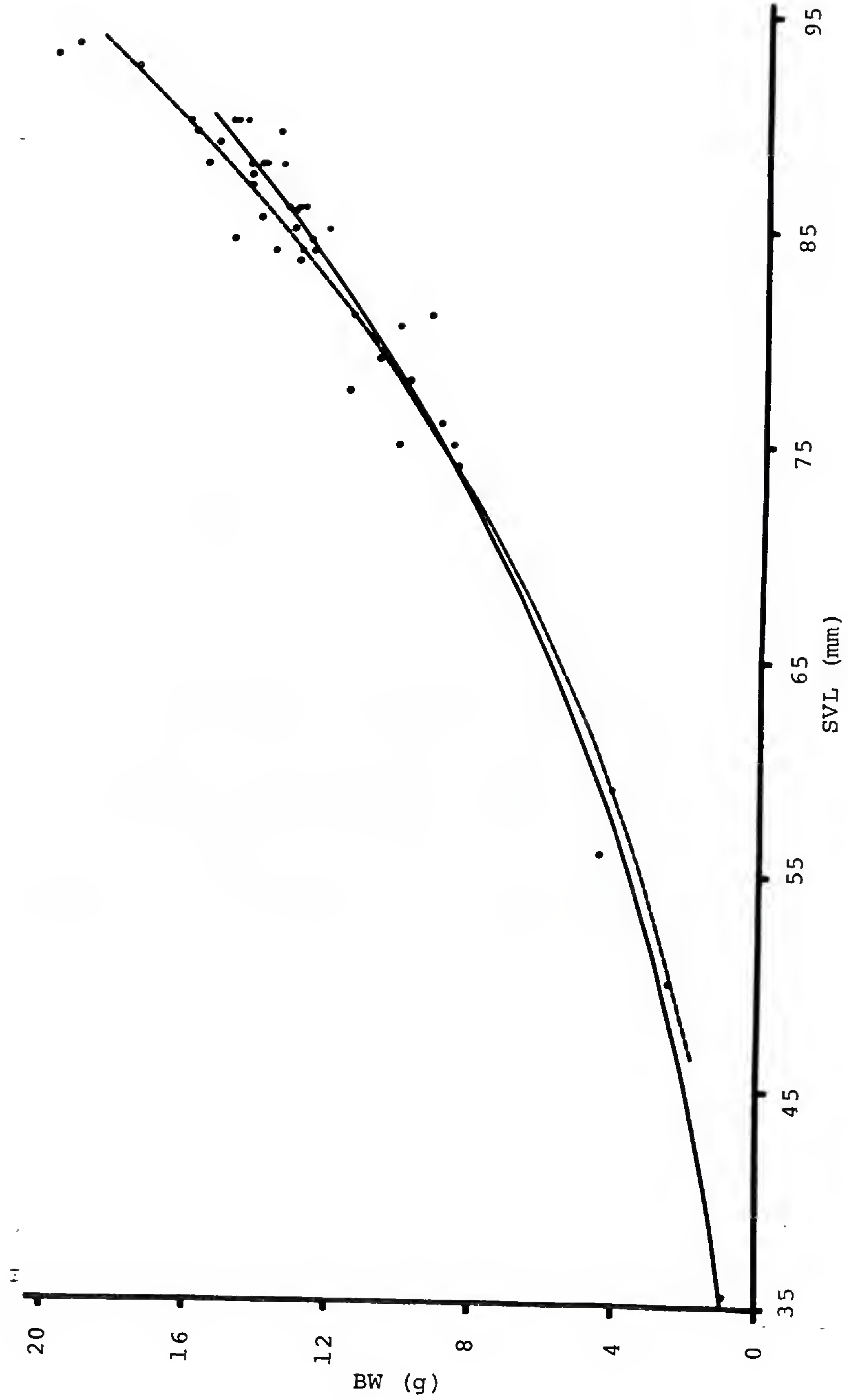
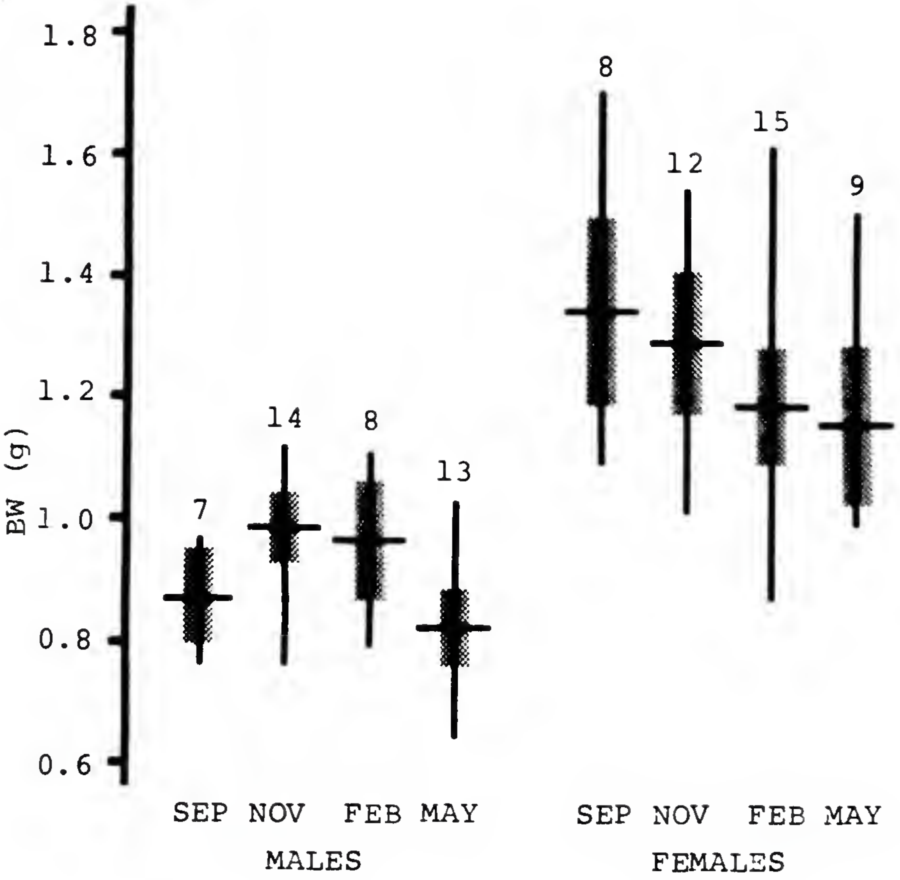

BW (g)
0
4
8
12
16
20
SVL (mm)
35
45
55
65
75
85
95

FIGURE 4-12. Seasonal Variation in Size of *Anolis humilis*. For the longest third of each sample, mean body weight (BW) and mean snout-vent length (SVL) are given as horizontal lines. Stippled bars indicate 95% confidence intervals; vertical lines show the range; and sample sizes are given by numerals above the range.


BW (g)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
7
14
8
13
8
12
15
9
SEP NOV FEB MAY
MALES
SEP NOV FEB MAY
FEMALES

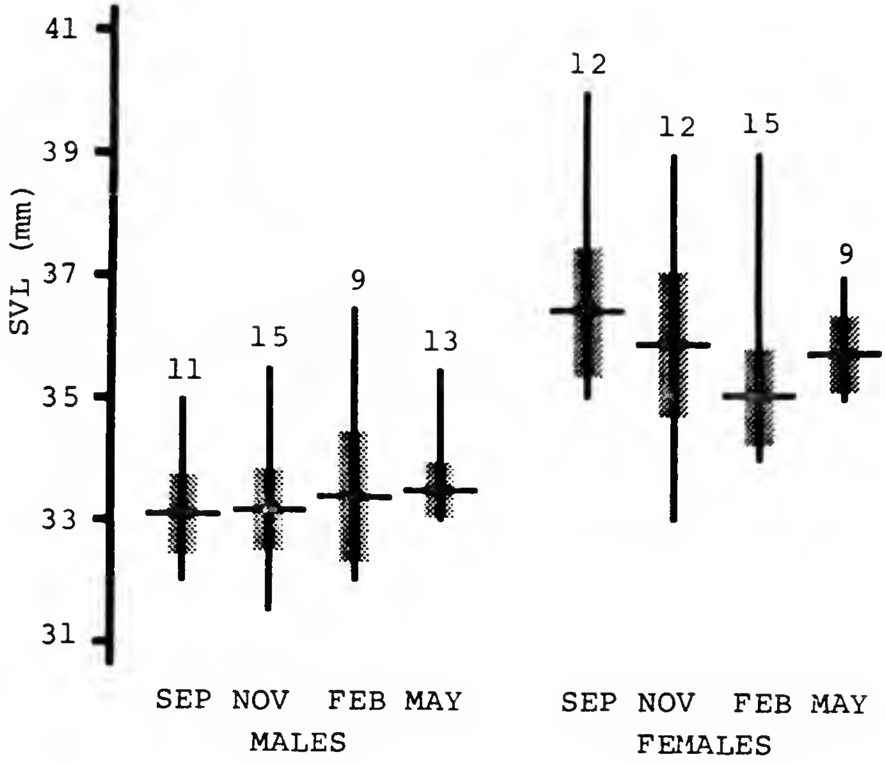
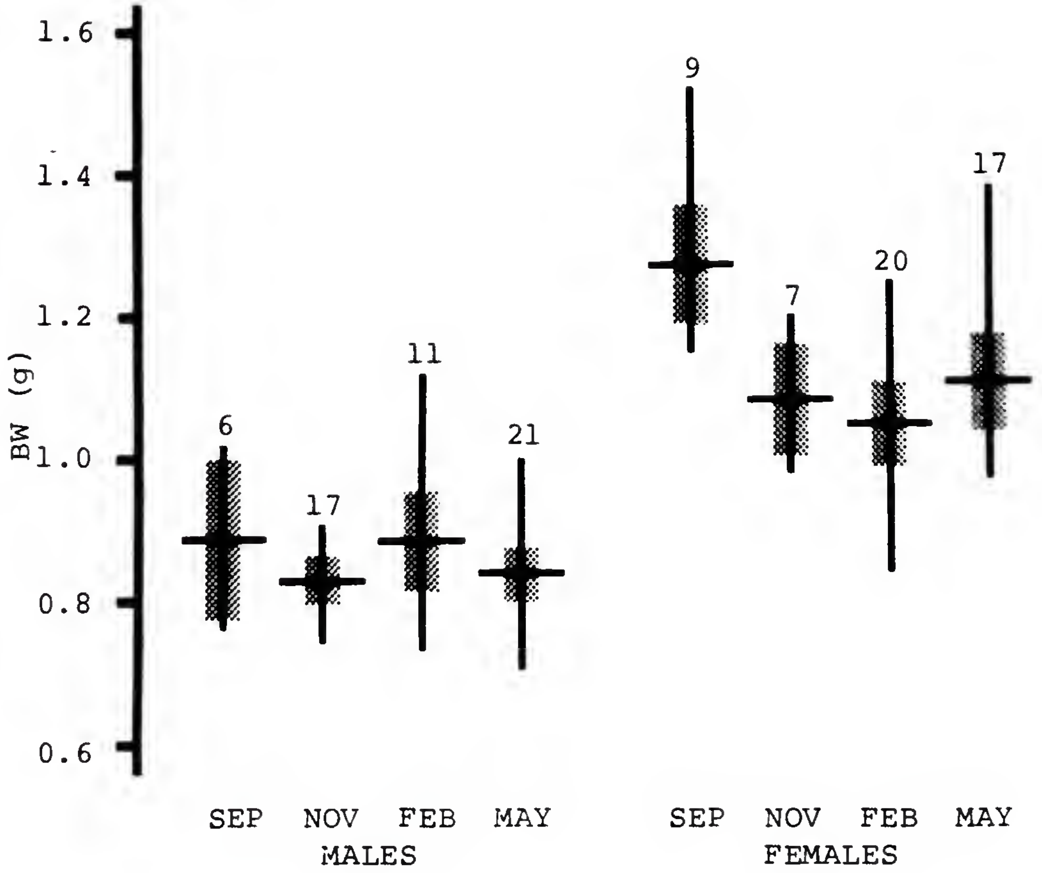

SVL (mm)
41
39
37
35
33
31
11
15
9
13
12
12
15
9
SEP NOV FEB MAY
MALES
SEP NOV FEB MAY
FEMALES

FIGURE 4-13. Seasonal Variation in Size of *Anolis limifrons*. Symbols are as in figure 4-12.


BW (g)
1.6
1.4
1.2
1.0
0.8
0.6
6
17
11
21
9
7
20
17
SEP
NOV
FEB
MAY
MALES
SEP
NOV
FEB
MAY
FEMALES

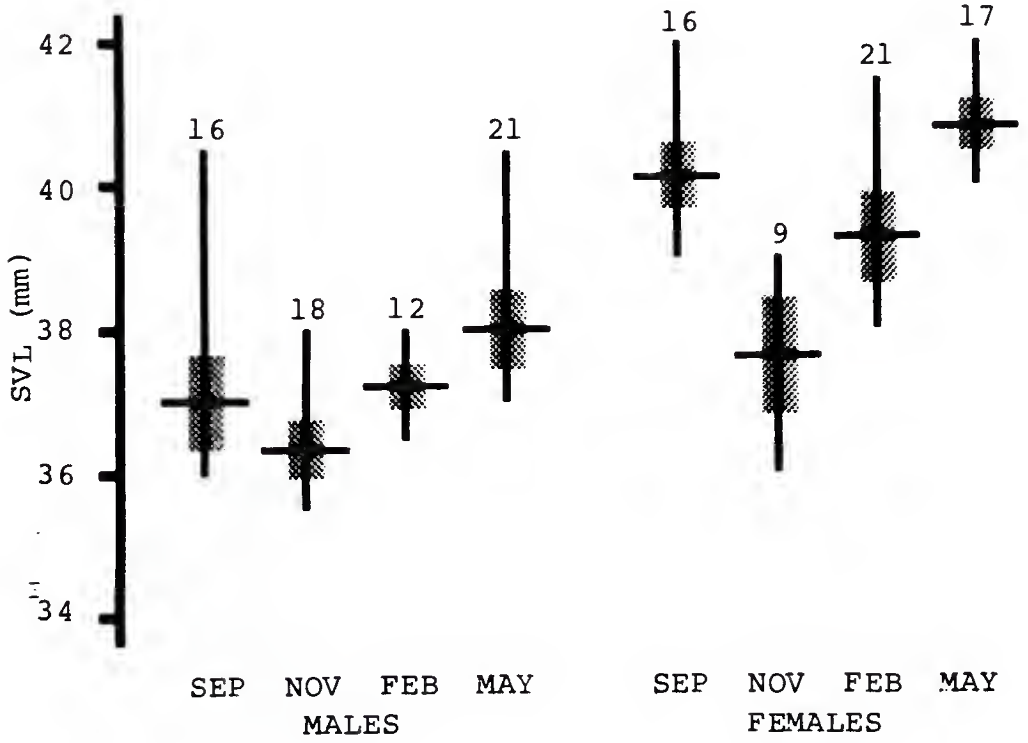
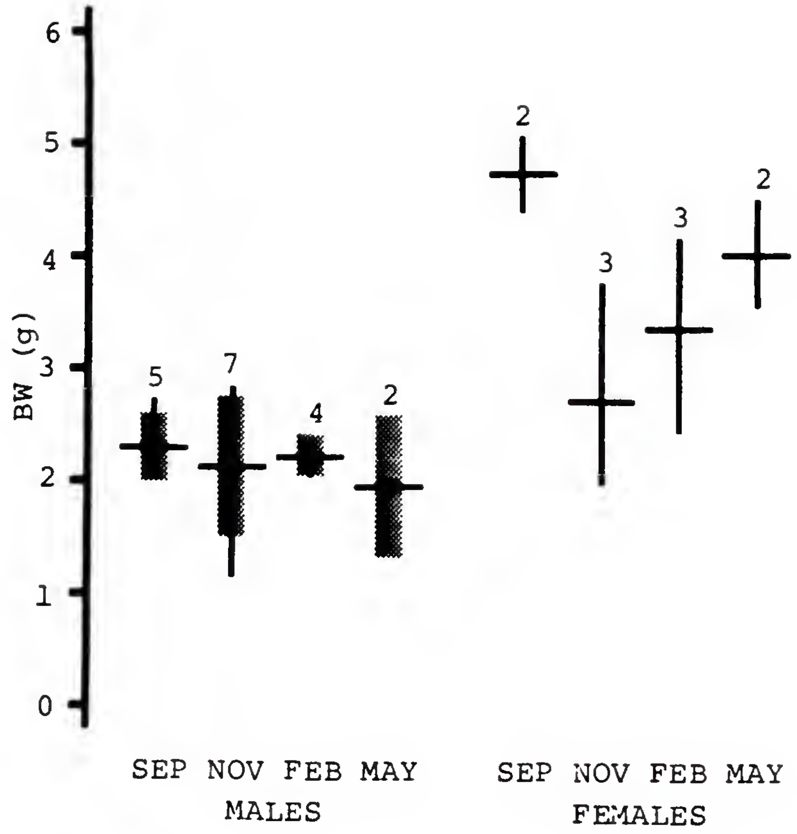

SVL (mm)
42
40
38
36
34
16
18
12
21
16
9
21
17
SEP
NOV
FEB
MAY
MALES
SEP
NOV
FEB
MAY
FEMALES

FIGURE 4-14. Seasonal Variation in Size of *Anolis lemurinus*. Symbols are as in Figure 4-12.


6
5
4
3
2
1
0
BW (g)
5
7
4
2
2
3
3
2
SEP NOV FEB MAY
MALES
SEP NOV FEB MAY
FEMALES

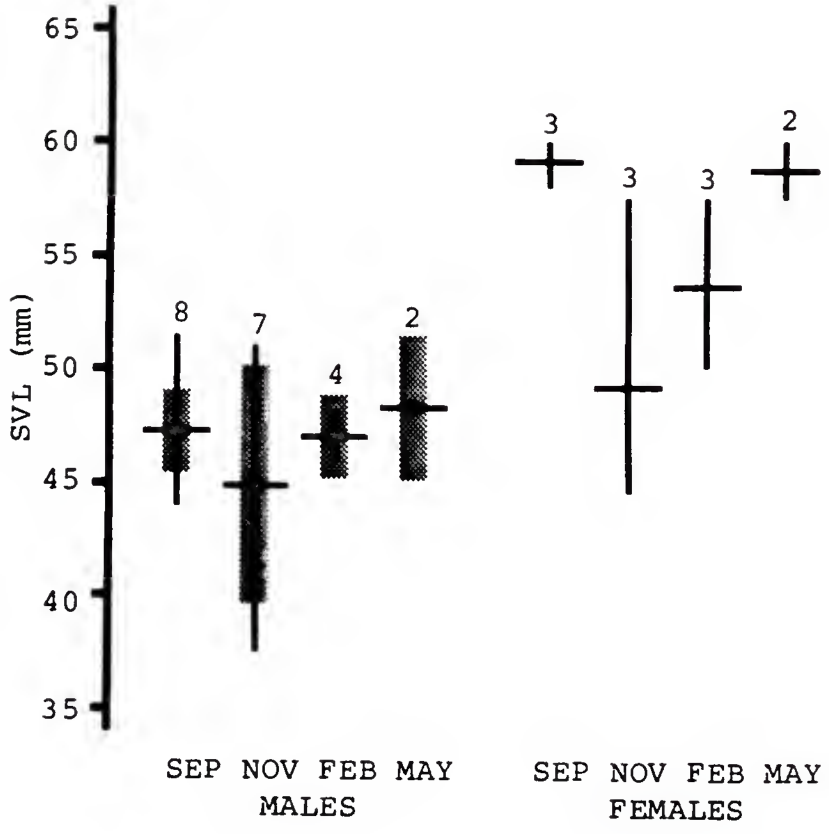
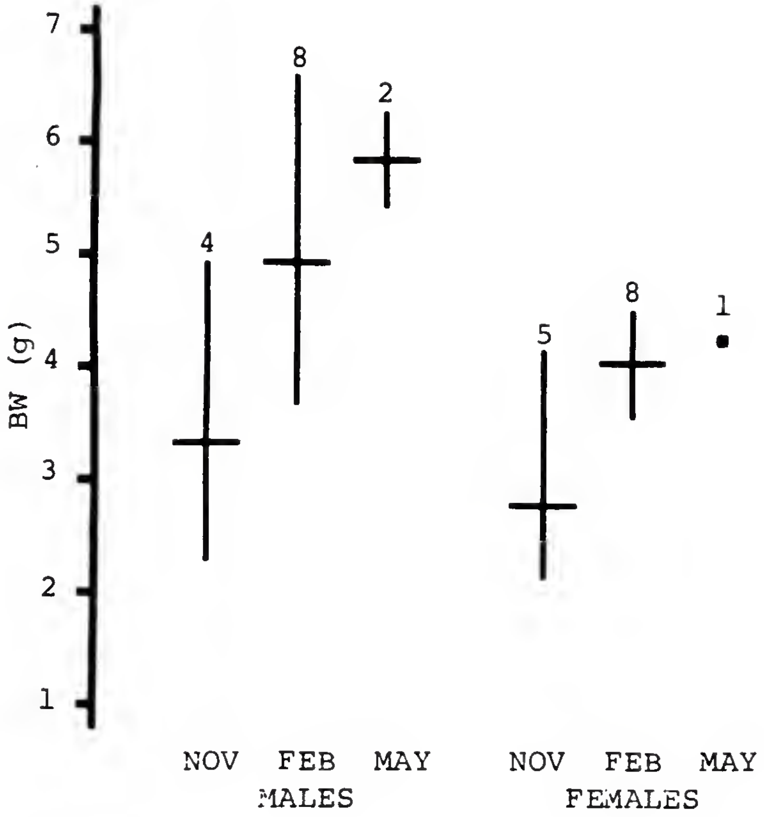

65
60
55
50
45
40
35
SVL (mm)
8
7
4
2
3
3
3
2
SEP NOV FEB MAY
MALES
SEP NOV FEB MAY
FEMALES

FIGURE 4-15. Seasonal Variation in Size of *Anolis lionotus*. Symbols are as in figure 4-12.


BW (g)
7
6
5
4
3
2
1
8
2
4
5
8
1
NOV
FEB
MAY
MALES
NOV
FEB
MAY
FEMALES

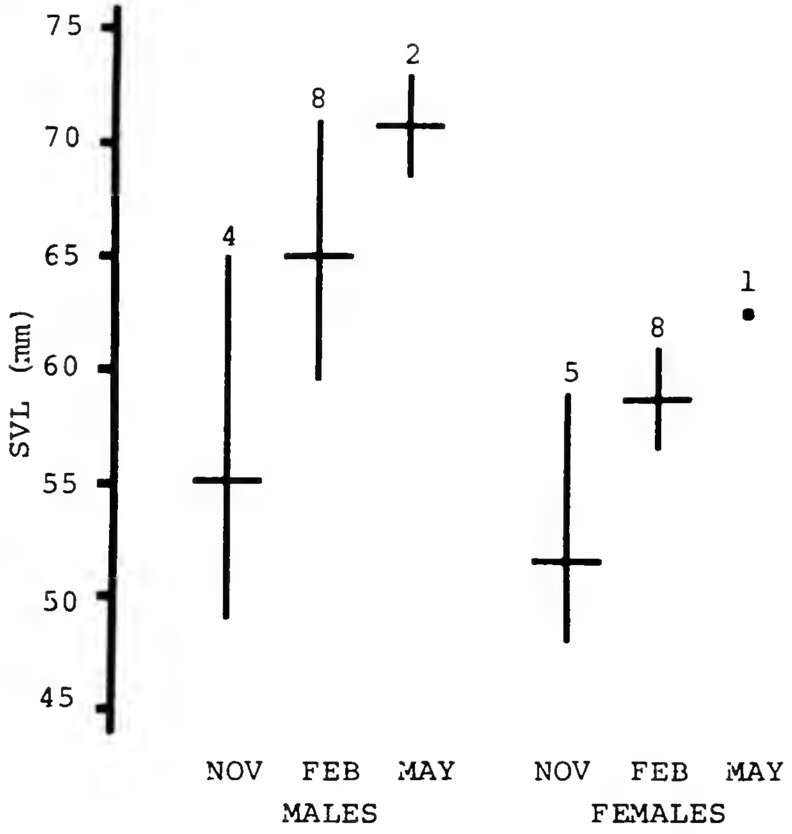

SVL (mm)
75
70
65
60
55
50
45
2
8
4
1
8
5
NOV
FEB
MAY
MALES
NOV
FEB
MAY
FEMALES

FIGURE 4-16. Seasonal Variation in Weight-Length Curves for *Anolis humilis* Males and Juveniles. Curves were fit for each period by least squares to the equation:

$$BW=aSVL^{b}.$$

Coefficients are given in the table 4-11. September curve is a solid line; November a dashed line; February a dotted line; and May a dot and dashed line.

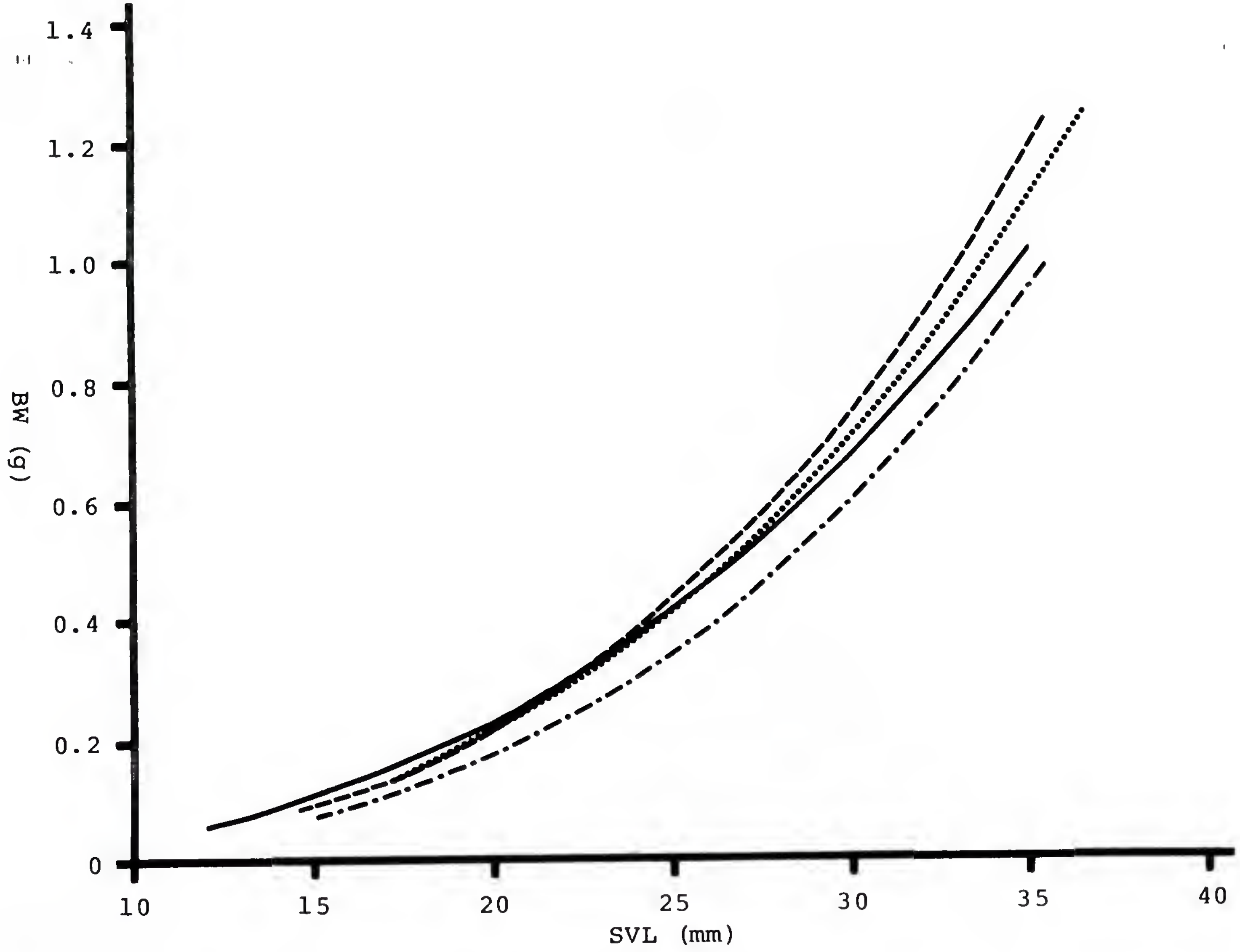

1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
BW (g)
10
15
20
25
30
35
40
SVL (mm)

FIGURE 4-17. Seasonal Variation in Weight-Length Curves for *Anolis humilis* Females and Juveniles. Curves are as in figure 4-16.

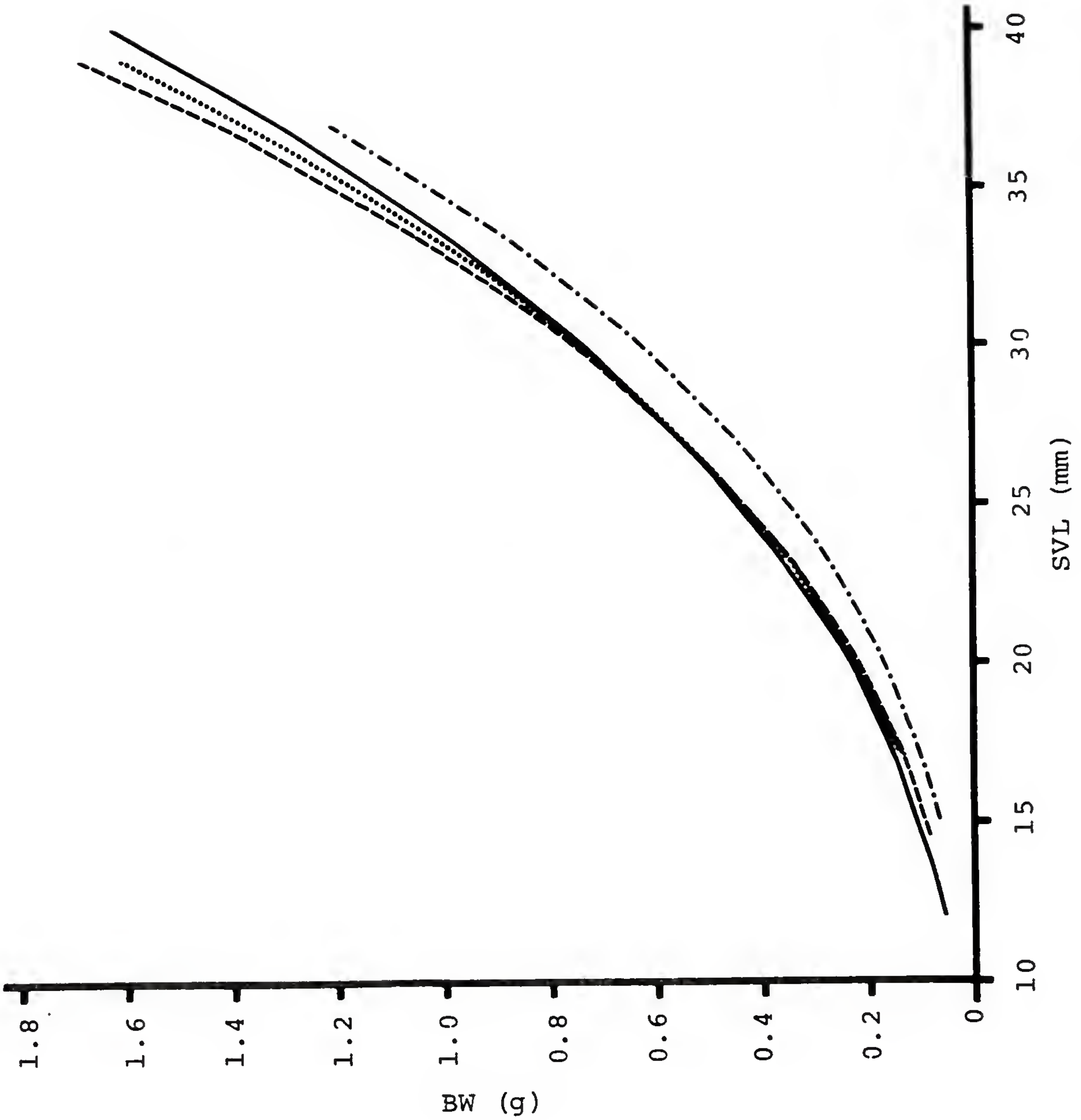

BW (g)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
SVL (mm)
10
15
20
25
30
35
40

FIGURE 4-18. Seasonal Variation in Weight-Length Curves for *Anolis limifrons* Males and Juveniles. Curves are as in figure 4-16.

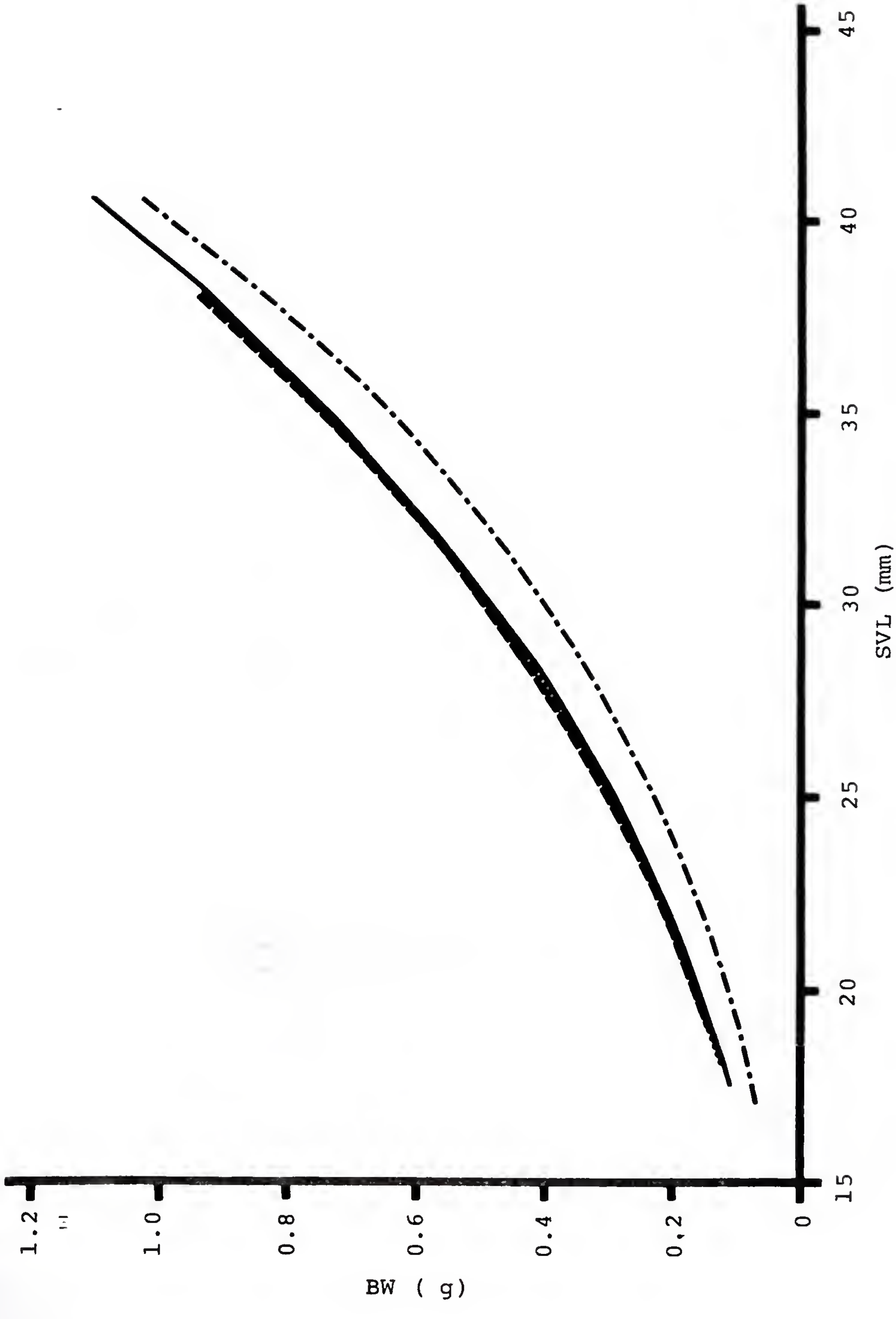

BW (g)
1.2
1.0
0.8
0.6
0.4
0.2
0
SVL (mm)
15
20
25
30
35
40
45

FIGURE 4-19. Seasonal Variation in Weight-Length Curves for *Anolis limifrons* Females and Juveniles. Curves are as in figure 4-16.

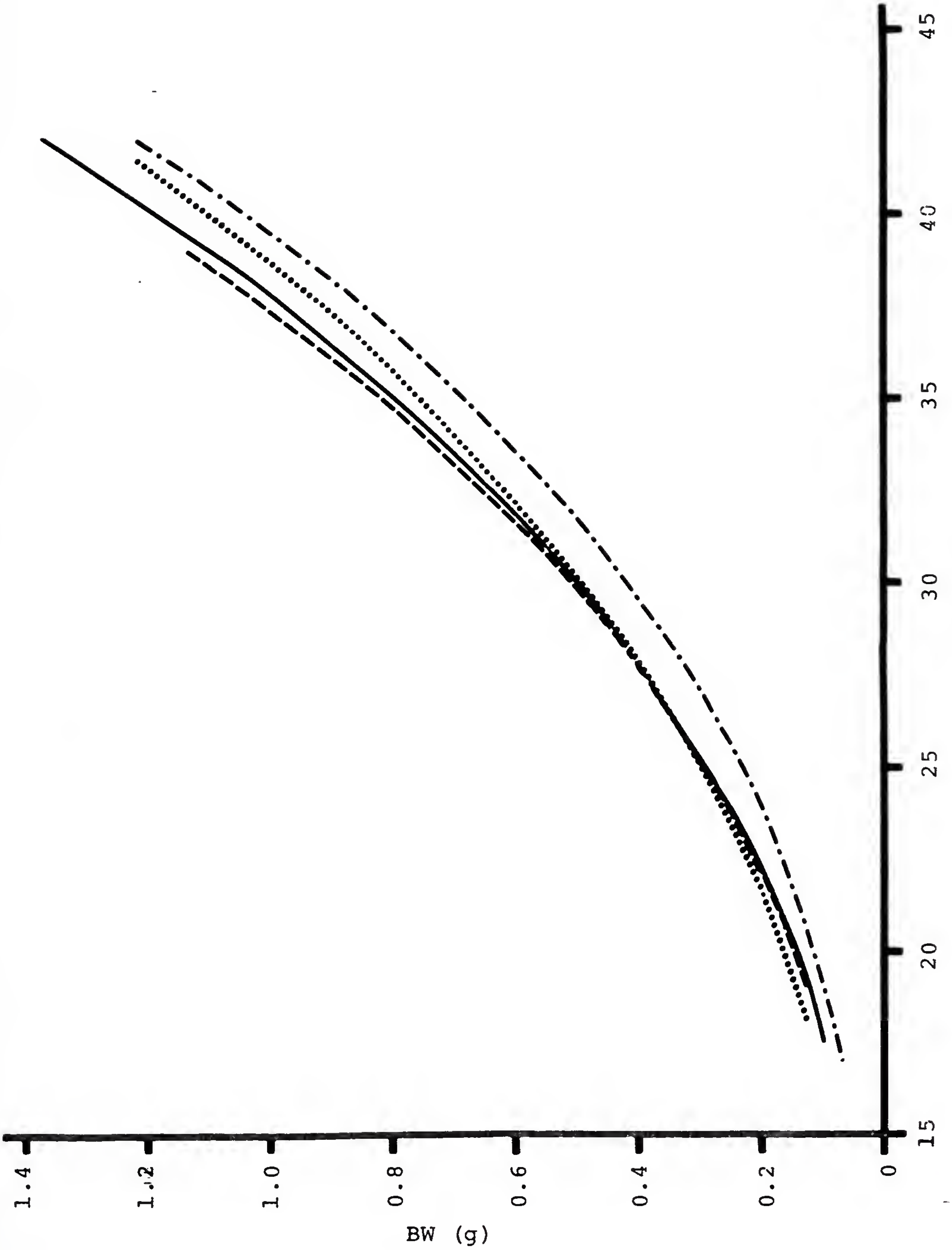

BW (g)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
SVL (mm)
15
20
25
30
35
40
45

FIGURE 4-20. Seasonal Variation in Weight-Length Curves for *Anolis lemurinus*, Both Sexes Combined. Surves are as in figure 4-16.

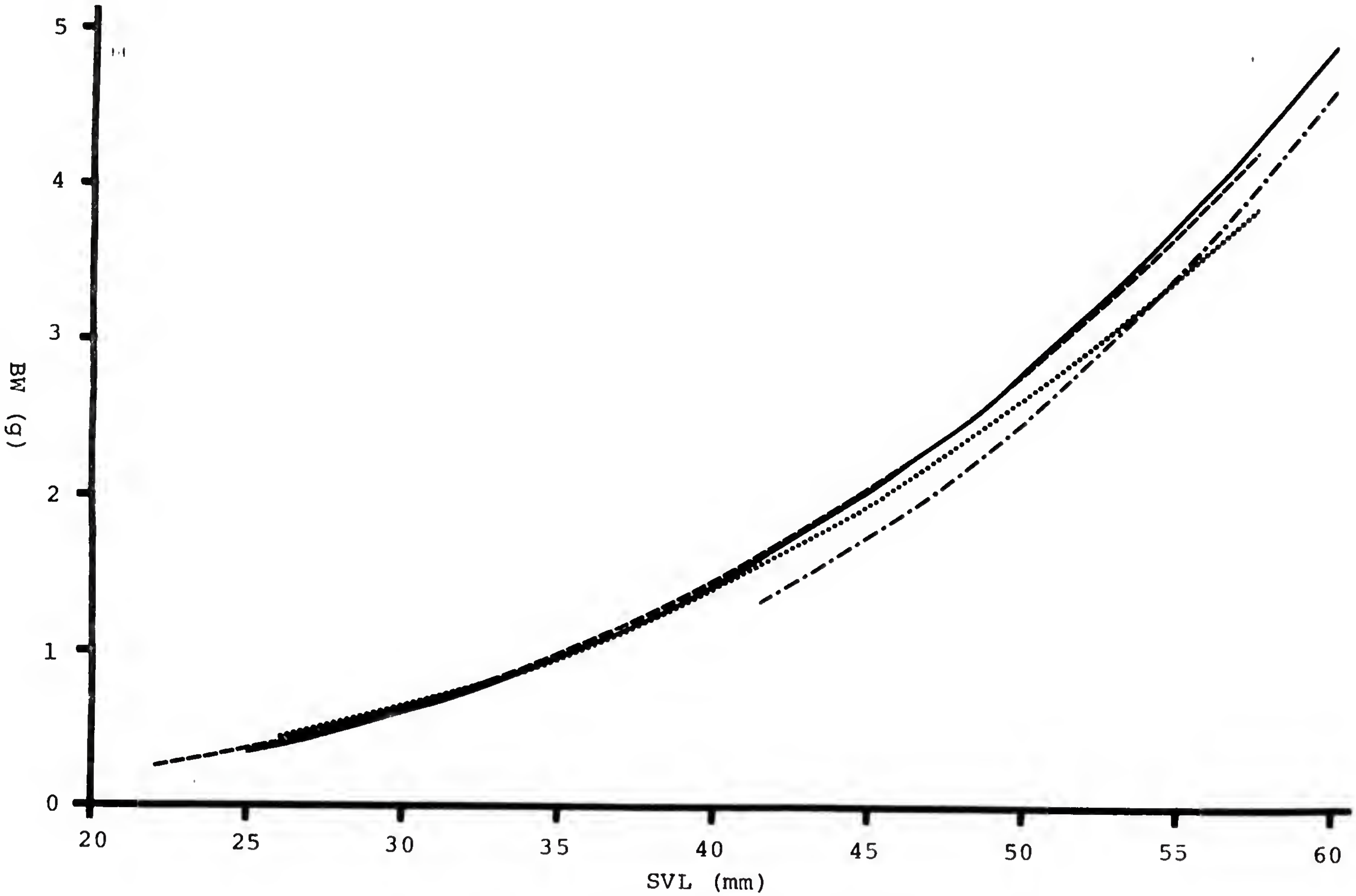
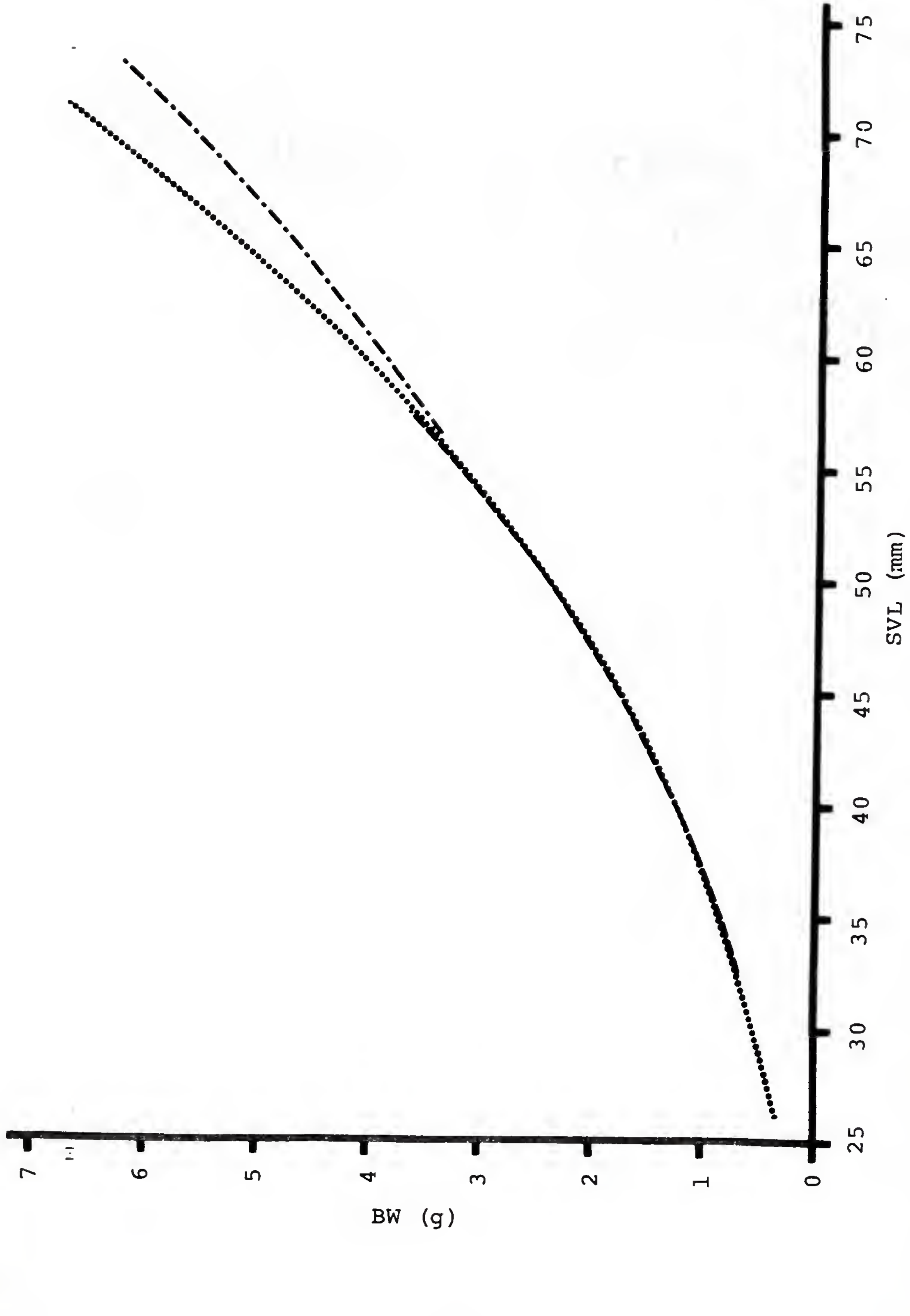

BW (g)
0
1
2
3
4
5
20
25
30
35
40
45
50
55
60
SVL (mm)

FIGURE 4-21. Seasonal Variation in Weight-Length Curves for *Anolis lionotus*, Both Sexes Combined. Curves are as in figure 4-16.


BW (g)
0
1
2
3
4
5
6
7
SVL (mm)
25
30
35
40
45
50
55
60
65
70
75

V. FOOD

1. Introduction

Anolis lizards are predators on small arthropods and, occasionally, other small animals. As such, prey selection and capture are important parts of their ecology. An anole typically perches in some characteristic location and, upon visually locating a moving prey item, rushes over to it, consumes it, and moves back to its perch. This type of food search and capture may occupy as little as 20% or virtually 100% of the activity period of some anoles (Andrews, 1971a; Fleming and Hooker, 1975).

Prey size and type has been considered for a number of West Indian *Anolis* species (Rand, 1967b; Schoener, 1967, 1968; Schoener and Gorman, 1968) and has been found to be an important aspect of ecological separation in sympatric species. Mainland anoles have been considered from this point-of-view in comparatively few papers. Sexton et al. (1972) and Fleming and Hooker (1975) discussed prey in a single species, and considered the effect of seasonality. Andrews (1971a) compared the diets of two *Anolis* species in southwestern Costa Rica, and considered the effect of lizard size on prey size. Only Duellman (1978) has considered food preference in more than two mainland species, and his discussion was only a limited portion of a much broader study.

This section will include the findings on prey size and taxa of the Río Frío anoles. In addition to simple enumeration of prey, similarity (Schoener, 1968) and overlap (Hurlbert, 1978) will be considered.

2. Materials and Methods

Lizards were collected as described in section IV, preserved in 10% formalin, and later stored in 40% isopropanol. The stomach of each lizard was removed, opened, and the contents were transferred to small glass vials of 70% ethanol for later examination. Because various kinds of prey items might be digested at different rates (Jackson et al., 1974) and because the rate of movement of items through the gut is dependent on size, only food items in the stomach or esophagus were counted and measured.

Prey items were identified and cataloged in the categories given in tables 5-2 through 5-9. The selection of categories is somewhat arbitrary. Ideally prey would be categorized with regard to it's perception by the lizards--flying vs. non-flying, hopping vs. crawling, fast vs. slow, hard vs. soft, odiferous vs. non-odiferous. However, this type of discrimination is largely precluded by the available information on neotropical insects, by the extremely large number of species of prey items, and especially by my knowledge of the habits of these prey animals. As a second choice, the more easily discriminated taxa do provide some of the desired attributes--most beetles are hard, flies fly, lepidoptera larvae are soft and wiggly, spiders are soft and crawl rapidly. Some taxa, the members of which were eaten very infrequently, were combined into a "miscellaneous" group. Arthropods which could not be positively identified (<1%) were placed in a separate category.

Each arthropod prey item was measured to the nearest 0.1 mm using an ocular micrometer in a Bausch and Lomb dissecting microscope. Length was measured from the head, not counting the antennae, to the tip of the abdomen, not counting the wings or ovipositor. Width and depth were recorded as "averages" to simplify the estimation of prey volume. Vertebrate prey items were measured with vernier calipers, with SVL used as the prey length measurement.

Size categories are also somewhat arbitrary in nature. One millimeter wide classes were chosen primarily for ease in comparison of this with other studies which have used similar categories. Since insect sizes are approximately log-normally distributed, some equal number of ln prey length might have been used, but this would make comparison difficult. Because arthropods become less and less common as their lengths increase, classes for those over 15 mm were combined to form wider, but still infrequently used, categories.

Snout-vent length of the anoles were measured to the nearest 0.5 mm before the lizards were preserved. Head length, head width and head depth were measured to the nearest 0.1 mm with vernier calipers after the lizards had been preserved in formalin and transferred to alcohol. Exact descriptions of these measurements are given in Appendix 1.

Because of the biological and semantic difficulties of establishing size classes that can be realistically labeled as adult, subadult or juvenile (see Section 4-2), both sexes of each species were divided into large, medium and small size classes in the following manner. All specimens in the group being considered were ordered from longest to shortest. The length of the individual that was one third of the number of specimens from the longest was used as the lower limit for the "large" sample. All specimens of that length or greater are included in that category. Similarly the length of the individual that was one third of the number of specimens from the shortest was used as the upper limit for the "small" sample. All specimens of that length or shorter are included in the "small" category. All other specimens are in the "medium" size class. The sex of very small specimens of *A. humilis* and *A. limifrons* could not be determined accurately. Because of this, additional size classes were established to include *A. humilis* of less than 20 mm SVL and *A. limifrons* of less than 23 mm SVL. These are designated "unsexed juveniles."

3. Indices of Resource Use

Many indices have been developed to compare resource utilization by two species or intraspecies groups. Hurlbert (1978) provided a thorough, critical review of many such indices, and proposed a new set based on Lloyd's (1967) earlier index for interspecies patchiness. The indices to be used here are described below.

The similarity(D) of prey of two groups will be expressed by the following:

$$D = 1 - \tfrac{1}{2} \sum_i \left| P_{xi} - P_{yi} \right| \qquad (1)$$

where Pxi and Pyi are the frequencies of items in the ith category for groups x and y respectively. This measurement has been used in anole studies (Schoener, 1968; Andrews, 1971a) and many others as a measurement of overlap. As suggested by Hurlbert (1978), however, this will be termed similarity and used to describe the degree of co-occurrence of taxa or sizes in the diets of two groups without regard to the availability of those prey items.

The overlap(L) of prey of two groups will be expressed by Hurlbert's (1978) equation:

$$L = \left[\Sigma(x_i y_i / a_i)\right] /100 \qquad (2)$$

where xi and yi are the percentages of items in category i used by groups x and y respectively, and ai is the abundance (percentage) of the resource found in category i. Hurlbert defines overlap, as "the degree to which the frequency of interspecific encounter is higher or lower than it would be if each species utilized each resource state in proportion to it s abundance." Thus, dietary overlap, to be considered here, is not merely similarity of prey type, but a measurement based on the proportion of shared prey types relative to the abundance of those prey types. It is expressed in the following manner: the likelihood that an individual of species (or group) x and an individual of species y will attempt to utilize the same food item within some time interval is L times as high as it would be if both species were perfect generalists, i.e. both utilized the resource states in proportion to their abundance. It is also evident that if two species have a certain similarity of usage of a relatively common prey item, their overlap (L) will be much lower than if they have the same similarity of use of a rare prey item.

Niche breadth (B) is a term commonly used to describe some range of resource use from the very limited (specialist) to the very broad (generalist). The expression used here to quantify niche breadth is Hurlbert's:

$$B = 100/ \Sigma(x_i^2/a_i) \qquad (3)$$

where xi is the percentage of items in category i used by group x, and ai is the percentage of the resource found in category i. This index can range from a minimum /100, when only the most rare prey type is eaten, to 1.0 when each prey type is used in proportion to its abundance. In addition, it sould be apparent that B will be lower for specialists on rare prey types than for specialists on common prey types.

The reciprocal of niche breadth is selectivity (G) (Hurlbert, 1978) which is not only an index of how selective a group is at choosing its prey, but also the frequency to which intragroup encounter is higher or lower than it would be if the group used each prey type in proportion to its abundance. It can then be said that "the probability of two individuals of this group attempting to utilize the same food item simultaneously is G times as great as it would be if members of that group were perfect generalists, i.e. utilized each prey type in proportion to its abundance." Selectivity is obtained thus:

$$G = 1/B = \left[\Sigma(x_i^2/a_i)\right] /100 \qquad (4)$$

where the symbols are as given above.

The major refinement in Hurlbert's indices (L, B, and G) is their inclusion of the variation in resource state availability. While this may provide a more biologically reasonable measurement, it also requires assessment of the real availability of those resource states to the organisms being considered. In many cases, such as the present study, that may be virtually impossible.

The most logical way to determine prey availability might be simply to sit or walk through the area, counting all potential prey items. This method has several deficiencies. First, it would take an inordinantly long time to sight enough prey items to adequately represent the resources available, expecially in a tropical forest. Second, the observer would probably not spot items from the same perspective as the lizards, their differing possibly in the ability to distinguish size, motion and color. The third drawback of this method is that one could never adequately survery above the ground or low trunk level. Even if insects were surveyed on recently felled trees, there would be an overrepresentation of the wood boring beetles and others which are attracted very quickly to broken branches.

Because an unbiased assessment of real prey availability seems impossible, it was decided to use an admittedly biased, but standardized survey of rain forest insects. Janzen and Schoener (1968) made sweep sample collections in a forest near Guapiles, only about 16 km SE of Río Frío. They did not intend for their study to be taken as an absolute determination of a tropical forest arthropod community, and they discuss fully the many biases of such sampling. Yet, it is as good a sample as anything available (probably the only such survey available for Costa Rica), so with biases in mind, it will be used for prey length categories (Table 5-1).

For prey taxa, a leaf litter survey (Andrews, 1971a) is available to compliment the foliage collections of Janzen and Schoener. Andrews mader her collections in a mature lowland forest on the Pacific side of Costa Rica, but the distribution of taxa at the level considered here is probably very similar to that of the Caribbean side. Her categories were combined with Janzen and Schoener's, and the average percent is used as prey taxa availability (Table 5-2). For both taxa and length, any category used by the anoles, but not collected in the leaf litter or sweep samples was arbitrarily given the minimum value of other categories to avoid division by zero.

Because all of the above indices will be used for both prey taxa and prey length comparisons, the subscripts t and l will be used to differentiate between the two.

4. Intraspecies Comparisons by Size

Prey items of all eight species are listed by taxa (Tables 5-4 through 5-11) and prey length (Tables 5-12 through 5-19). The distributions of prey items by length are shown in Figures 5-1 through 5-12. Sample sizes of *A. pentaprion* and *A. capito* were too small for most intraspecies comparisons, so they are not included. Niche overlap, similarity, breadth and selectivity are listed for the other six species for frequency of prey taxa (Tables 5-20 and 5-21) and frequency of prey length (Tables 5-22 and 5-23). Because head size had been found to be closely related to prey size, regressions of head measurements on SVL are shown in Figures 5-13 through 5-20.

Prey Taxa.

Differences in prey taxa between intraspecies size classes are few. Similarity indices (Table 5-20) are generally quite high, indicating that most anoles of a species eat the same taxa of prey regardless of size. However, a few significant differences do occur.

It might be expected that juveniles would eat more of the small, soft-bodied prey, such as flies, barklice and termites; while adults would be expected to feed more often on the larger, hard prey items. To test this hypothesis, the distribution of certain taxa in the diets of small males and females (and unsexed juveniles of *A. humilis* and *A. limifrons*) combined were compared to the numbers of these taxa found in the large males and females combined. Significance of differences were determined by a 2 x 2 chi-squared test.

Anolis humilis is the only species in which termites were found and contrary to the expectation, large *A. humilis* contained significantly more termites than did small and juveniles ($P<.05$), although the number eaten was small. Both barklice and flies were eaten by *A. humilis* and were slightly more common in the small classes, but the differences were not significant. Large *A. humilis* did consume significantly more beetles ($P<.05$) and ants ($P<.05$) than did small.

Anolis limifrons small classes ate significantly more flies ($P<.001$) and barklice ($P<.001$) than did large classes. Large *A. limifrons* ate more beetles and spiders than did the combined small group and the differences are significant ($P<.01$ for beetles, $P<.05$ for spiders). However, a single large female *A. limifrons* contained 21 small beetles of apparently the same species, if these 21 items from the same stomach are excluded, or counted as a single item the difference is not significant. Likewise, a single large female contained 21 spiders, 19 of which were of the same small species. If these 19 spiders are excluded or counted as a single item, the difference in spiders is also not significant.

The only significant difference between large and small *A. carpenteri* is that the small ate snails and the large did not ($P<.01$). This difference is less interesting when one considers that the sample size is very small and that there were very few juvenile *A. carpenteri* collected, so the actual size difference between the small and large classes is not great.

A. lemurinus shows several significant size related prey taxa differences. Small *A. lemurinus* ate significantly more flies ($P<.05$) and barklice ($P<.001$) than did large classes. Again, however, one of these differences can be attributed to a single individual's concentration of a single food item. All 22 barklice eaten by *A. lemurinus* were in the stomach of a single small male. If these are excluded or counted as a single item, the difference disappears. Large *A. lemurinus* fed significantly more often on members of three taxa: Coleoptera ($P<.01$), Orthoptera ($P<.05$), and Formicidae ($P<.05$). Small anoles might be expected to avoid these because the beetles are too hard, large Orthopterans too difficult to subdue and swallow, and many ants either sting or are distasteful.

Small *A. biporcatus* took significantly more beetles than did large members of that species. In fact, with beetles making up more than 50% of the prey items in small males and 35% in small females, small *A. biporcatus* had the most taxonomically restricted diet of any size class of any Río Frío *Anolis* species, except for small *A. pentaprion.* In the latter species, only 12 prey were found in the small classes, but 7 of the 12 (58.3%) were flies. Large *A. biporcatus* frequently ate very large ants, so the total number of ants eaten by them is significantly greater ($P<.001$) than the number eaten by small *A. biporcatus*.

In none of the other numerous comparisons is there a significant difference in the number consumed by large members of a species compared to small and juveniles of the same species. If volume of prey were considered instead of number of items, some of these differences might change in significance.

Hurlbert's (1978) niche overlap (L) and niche breadth (B) provide another way to compare prey use between and within anole size classes. The niche overlap between intraspecies size classes is rather high ($\bar{L}_t=6.05$) for *A. humilis*. This index means, for example, that the likelihood that a large male *A. humilis* and a large female *A. humilis* will attempt to utilize the same food item is 4.84 times as high as it would be if both utilized the prey items in proportion to their abundance. Why is this so high? Since all classes of *A. humilis* feed on most categories of prey, should not the overlap between such generalists be low? The answer has to do with prey abundance. Comparison of Tables 5-1 and 5-4 will show that all size classes of *A. humilis* prey on isopods considerably more than would be expected from the abundance of this prey taxa. This "over-use" of a "rare" food type means a higher overlap index and, presumably, more competition for those items. The same is true of *A. humilis*' "over-use" of Coleoptera larvae and Lepidoptera larvae. On the other hand, their more extensive use of even more common taxa, e.g.

spiders, beetles, has little effect on the overlap index. Because those items are very common, the lizards don't really compete for them, they simply draw from the same abundant resource. Hurlbert's index should prove quite useful in reaffirming the distinction between competition and similarity of resource use.

Within the series of L_t values for *A. humilis*, there is only slight variation. The highest values are for comparisons of unsexed juveniles with all other classes. This is, again, because unsexed juveniles feed most heavily on the less common taxa. Almost 50% of the prey of the smallest *A. humilis* are from four taxa (Coleoptera larva, Lepidoptera larva, Diptera adults and Isopoda) making up less than 9% of the available resource. From the most common groups (Formicidae, Coleoptera adults and Araneida) which make up almost 70% of the available prey, they derive only about 30% of their food items. Unsexed juvenile *A. humilis*, as a result, also have the lowest B_t of any size class of that species. Thus, where similarity of diet occurs between juveniles and other classes of *A. humilis*, it is most likely to be at those rare prey classes, thereby causing the highest overlap values.

Size classes of *A. limifrons* also have very similar diets, in fact, significantly higher S_t's than *A. humilis* ($P<.001$, Mann-Whitney test). All classes of *A. limifrons*, however, prey less often on the less common prey taxa, relying more heavily on the abundant beetles, spiders and orthopterans.

As a result, even though S_t is high for interclass comparisons within *A. limifrons*, overlap is low; and nich breadth is high. L_t's are significantly lower for interclass comparisons in *A. limifrons* than in *A. humilis* ($P<.001$, Mann-Whitney test). In *A. limifrons* highest overlap values are for small males compared with all other classes, primarily because of their high use of Lepidoptera larvae.

Similarity is lower between the classes of *A. carpenteri*, and overlap is variable. The only point of interest is the finding of snails in the stomachs of several individuals, including two small males, a small female and a medium male. The small sample sizes, coupled with the presence of these items, which are "rare" according to Table 5-2, causes very high overlap values when these classes are compared and high B_t's for the small classes. Actually snails are probably much more common than the table indicates. That number is simply an arbitrary result of the process by which taxa not considered by Janzen and Schoener (1968) or Andrews (1971a) were assigned values. On the other hand, snails are certainly not as available to anoles as their numbers might indicate since they are primarily secretive and nocturnal.

Overlap between classes of *A. lemurinus* is very similar to that between classes of *A. humilis* for much the same reasons. Only one comparison, medium males versus small females, is much higher than the others. Snails and beetle larvae are the two categories of overlap that contribute most to this value.

Within *A. lionotus*, the riparian anole, B_t is very low in all classes except medium males. While, in part, this must be due to their preferred feeding on less abundant prey types, it also may be due to the small prey samples for each class. *A. lionotus* probably is as general a feeder as is *A. limifrons*, but because only a small number of items was found for each class, some comparisons give very low L_t's, and some, where both ate much from the less abundant prey classes, give very high L_t's. Similarity is also quite variable, but not as much as L_t, since S_t does not consider prey abundance.

A. biporcatus is more like *A. humilis* or *A. limifrons*, a generalist with moderate use of less abundant prey types. Extreme values in L_t, B_t and G_t for *A. biporcatus* all involve medium females, and are due to their higher predation on Lepidoptera larvae and vertebrates, primarily other anoles.

In general, similarity of prey taxa is high within species. Overlap is consistently higher than 1.0 because of the frequent use of less abundant prey taxa by all classes of all species. All classes of all species utilize ants as food less than proportionally to their abundance, thus contributing to L_t's higher than 1.0. Extremes in intraspecific variation in prey taxa can probably be attributed more to sample size than real differences in prey distribution between size classes. The means of the S_t's for each of the six species considered here are positively correlated to the number of prey items found ($r=0.025$, $P_{(r=o)}<.05$).

Prey Length.

Prey size of anoles and other small predators (Schoener, 1967, 1968; Hespenheide, 1971) is not normally distributed, but generally skewed to the left. Length distributions become more normal as anole size increases, and volume distributions may be right skewed in larger species. This distribution is similar to the distribution of arthropod sizes (Schoener and Janzen, 1968; Janzen and Schoener, 1968). Inspection of Figures 5-1 through 5-21 will show that prey distributions of Río Frío *Anolis* seem to fit that pattern. Because of this kind of distribution, mean prey lengths should be compared with reservation, because they are usually longer than the most commonly eaten prey (Figures 5-1 through 5-12). Therefore, for statistical comparison of prey size, the Kolmogorov-Smirnov test is used to compare the cumulative frequency of items by size.

Several studies have shown that classes of large anoles usually eat larger prey items than do classes of smaller anoles (Schoener, 1967, 1968; Schoener and Gorman, 1968; Andrews, 1971a; Sexton et al., 1972). This appears to hold true for Río Frío *Anolis*, but few differences are significant, and in two comparisons, the larger class takes significantly more small prey. The significance of all intraspecies comparisons of prey length distributions (Kolmogorov-Smirnov-one-tailed test) are given in Table 5-24. Prey length by volume distributions tend to spread any differences since the less often consumed long prey items increase in volume more than do shorter items. As a result volume distributions show more differences than do item distributions.

Large males have more large items in their diets than smaller males and unsexed juveniles. Item distribution comparisons of large males with other classes of smaller males show that the differences 1) are not significant for medium males in any of the six species compared; 2) are significant for only three species for small males; and 3) are significant for unsexed juveniles for both *A. humilis* and *A. limifrons*. Volume distribution comparisons show significant difference in all but three cases.

In most cases, like the males, long females eat more large food items than smaller females. However, for the item distributions, only in *A. humilis* is there a significant difference between large females and all other smaller classes. In *A. limifrons*, large females have significantly more long prey than unsexed juveniles ($P<.05$), but the difference is not significant for long vs. small females. Medium females have significantly more long prey items than do large females ($P<.01$). However, if the 21 small beetles from the stomach of one large female and the 19 small spiders from the stomach of another large female are deleted or counted as one item, large females then eat significantly more long items than small females ($P<.05$), and unsexed juveniles ($P<.001$), and the difference between large and medium is not significant.

Volume distributions for both *A. humilis* and *A. limifrons* show that large females get a significantly larger part of their volume of food from long prey items than do medium or small females or unsexed juveniles. Differences in volume are also significant for comparisons in *A. lemurinus, A. lionotus* and *A. biporcatus*. Neither item nor volume differences are significant for *A. carpenteri* females.

Overlap (L_1) is much greater between size classes of the larger species than the smaller. For the six species compared, the mean interclass overlap ($\overline{L}_1$) is positively correlated to both the $\overline{SVL}$ of the large males ($R=0.89$, $P_{(r=o)}<.05$) and the $\overline{SVL}$ of the large females ($r=0.94$, $P_{(r=o)}<.01$). Larger species have very high L_1's between classes because they overlap at the less common, large-size prey. The smaller species, *A. humilis, A. limifrons* and *A. carpenteri* have L_1's that are much closer to 1.0 because all interspecies size classes feed primarily on the small, common items. Overlap at these prey classes contributes little to an increased L_1. Interclass similarity (S_1) is apparently not related to species size. Correlations between mean interclass similarity ($\overline{S}_1$) and $\overline{SVL}$ were not significant for either large males ($r=-0.80$, $P_{(r=o)}<.05$) or large females ($r=-0.76$, $P_{(r=o)}<.05$).

Because it is affected in a similar way by prey abundance, the niche breadth index (B_1) is also related to the size of the lizards. Those classes which concentrate on the common, small prey itesm should have higher B_1's than those which prey primarily on large, rare items. B_1 would then be inversely correlated to anole size. Within the species, this is significant only for *A. biporcatus* ($r=-0.917$, $P_{(r=0)}<.01$), which has the greatest difference between $\overline{SVL}$ of all classes. For all size classes of all six species considered, the inverse correlation is highly significant ($r=-0.761$, $P_{(r=0)}<.01$).

Schoener has found for West Indian *Anolis* that

> within a given species in a particular area there is a linearly increasing relationship between the arithmetic mean of prey size and predator head length above a certain predator size; below that size, mean prey size decreases asymptotically. (1970: 15)

Discussions of predator size and prey size above have used SVL to represent predator size. However, HL is linearly related to SVL in most *Anolis*, including the eight species at Río Frío (Figures 5-13 through 5-20), so either might be an appropriate indicator of anole size. Figure 5-21 shows the relationship between mean prey length (PL) and head length (HL) for all eight species collected at Río Frío.

While there seems to be considerable departure from absolute linearity in the lines of Figure 5-21, I suggest that small samples of prey items are responsible for most of the variation. Table 5-25 shows the linear relationship between $\overline{PL}$ and HL (in 1 mm classes) for six Río Frío species. Classes with less than 5 prey items were ignored. *A. pentaprion* does not show a significant correlation, probably due to the small number of prey items found. Sample size was too small in all HL classes of *A. capito*.

5. Intraspecies Comparisons by Sex

In most Río Frío anoles, large females are significantly longer (SVL) than large males, and large females have longer heads. This is true for all except *A. lionotus* and *A. pentaprion* in which males are longer. Based on size alone, then one would expect large females to eat more large prey items than large males. This is not clearly the case.

In none of the six species considered, is there a significant difference between prey item distribution for large males and large females (Table 5-24). If volume of prey items is considered, then three of the species have large females which obtain a significantly greater proportion of their food volume from longer prey items than do large males. In two species there is not a significant difference, and in *A. humilis*, the smaller large males get significantly more prey volume from large prey items than do large females.

If $\overline{PL}$ of large males is compared (t test) to $\overline{PL}$ of large females (Table 5-26), differences are significant for only two species. Large male *A. pentaprion* eat significantly longer prey than large females ($P<.01$), and large female *A. carpenteri* eat significantly longer prey than large males ($P<.05$). In both of these species, the larger sex is eating larger prey.

Since large males of most Río Frío anoles are smaller than the large females, yet do not usually take smaller prey, it might be expected that large males would take larger prey when compared to females of the same size range as the large males. (The situation is exactly reversed in *A. lionotus* and *A. pentaprion*, in which males are larger.) To determine this, prey distributions and mean prey lengths were calculated for all females falling within the SVL range of the large male classes (males falling within the SVL range of the large female class for *A. lionotus* and *A. pentaprion*). These groups include many of the same animals included in the large females classes, of course, because the large females and large males overlap considerably in SVL range (Table 5-3). Comparisons of prey distributions by item length (Kolmogorov-Smirnov one-tailed test) show that only in *A. biporcatus* is there a significant difference ($P<.05$), and as expected, large males take more large items than similar sized females. Comparison of $\overline{PL}$'s showed no significant differences in any of the five species with larger females (Samples of *A. capito* were inadequate for comparison) or either species in which males are larger.

Several other studies have found differences between prey size in large males and large females. In three species of West Indian anoles, in which the males are much larger than the females, Schoener (1967) and Schoener and Gorman (1968) found that adult females take smaller sized prey than either large adult males or males of the same sizes (subadult males) when the females were reproductively active. In three other species sampled when not reproductively active, Schoener (1968) found rapidly growing subadult males to take more small prey than fully grown, non-reproductive, adult females of the same size. They suggested that the comparatively greater demand of reproduction or growth mandated feeding on smaller, but more numerous prey items. Andrews (1971a), however, found adult females to take larger prey items than either the large adult males or equal sized subadult males in *A. polylepis*, regardless of season. She reasoned that females were forced to feed on large prey which contain more energy per item, to build fat reserves during the non-reproductive season and to sustain egg production during the reproductive season. Fleming and Hooker (1975) found no difference in prey size during the wet (reproductive) season for *A. cupreus*, adult males of which are slightly larger than females. During the dry season, they found that the females, which were not reproductively active, took prey significantly smaller than that of the males.

In all of the above instances, it was determined that reproductive females require some additional food. In two instances females take larger items (Andrews, 1971a; Fleming and Hooker, 1975). In the others, where smaller items are eaten, there is an increase in the number of items, for an overall increase in prey volume. In all Río Frío *Anolis* species, most large females contained oviducal eggs during all collecting periods, although there is some reduction in egg production during the dry season in most species (See section VI.). Since females apparently do not take longer prey than males, is there any difference in the number of items per stomach? The answer to that seems to be positive, with large females eating more items per meal than large males. Ignoring empty stomachs, the difference in the number of items per stomach is significant only for *A. humilis* ($P<.05$, Mann-Whitney test) and *A. limifrons* ($P<.05$). The mean number of items is larger for females in all except *A. capito* (Table 5-26), but the small numbers of lizards with food obscured any differences in other species. If the sizes of items are not different, and females eat more items per unit time, then the prey volume per stomach should be higher for large females. Again the expectation is fulfilled; in all except *A. pentaprion* and *A. capito* which have extremely small samples, the mean prey volume per stomach is higher for large females than for males (Table 5-26). Differences are significant for *A. humilis* ($P<.05$, Mann-Whitney test), *A. limifrons* ($P<.01$) and *A. lemurinus* ($P<.001$).

6. Intraspecies Comparisons by Season

Both *A. humilis* and *A. limifrons* are "leaner" in the May collections than in any others. In section 4-6, it was suggested that a late dry season decline in food might account for this. In this section, seasonal variation in prey size, number and volume will be considered in those species, to determine if seasonal size changes are, in fact, reflections of seasonal variation in food.

Insect population studies have suggested a dry season decline in the numbers of small insects, so that the mean insect size increases (Janzen and Schoener, 1968; Schoener and Janzen, 1968). Since anole prey size is at least partially limited by anole size, small species such as *A. humilis* and *A. limifrons* should be most affected by any dry season decline in small prey. The effect expected would be an increase in prey length or a decrease in the number of items if there is no shift to larger prey.

Prey length of *A. humilis* and *A. limifrons* are given by collection period in table 5-27 and figure 5-22. Distributions of the prey by length are shown in figures 5-23 and 5-24. The expectation of longer prey in May is met only for female *A. humilis*, in which there are significantly more long items in May than either November or February. An additional difference which was not expected, is that September prey items are longer in females of both species. In *A. humilis* there are significantly more long items in September than either November or May, but not February; and in *A. limifrons* there are significantly more long items in September than in November or February. In contrast, there are no significant differences among the distributions of the males of either species.

The number of items per meal also is quite variable, and there are even fewer significant differences (Table 5-27). The only difference of significance is between September and May in female *A. limifrons*, with significantly more items per meal in September. Perhaps more indicative of food availability is prey volume per stomach (Table 5-27). Unfortunately this is a most variable measurement (Note the very high standard errors.), so few differences are significant. The May volume is significantly lower than either September or November in *A. humilis* females.

In the discussion above, and for computation of mean volume and number of items, empty stomachs were not counted. A lizard may have no food in its stomach for a variety of reasons not connected with prey availability. For example, it might have been collected early in the morning or on a cold, cloudy day; or it might have been collected in an area of just-felled trees, where it was too disturbed to feed. Though there are all of these possibilities, there is also the possibility that prey was not available. The former reasons should not be restricted to any one period, but should be evenly distributed. If, however, prey was less abundant in May, one might expect more empty stomachs in May, when compared to other periods. Table 5-28 shows that there are significantly more empty stomachs from May *A. humilis* and *A. limifrons* of both sexes, when compared to those from any other period. Also, in May *A. limifrons,* those with prey are significantly larger than those without prey ($P<.05$, Mann-Whitney test). Thus when food is scarce, the largest *A. limifrons* get that which is available. This difference, was not significant in May *A. humilis*, and such differences were not found in any other period for other species.

In general then, it does not appear to be a change in prey size that accounts for a May weight decline, although there is a non-significant decrease in some. Only female *A. limifrons* show the expected May increase in prey length. Likewise it does not seem to be due to the number of items or volume of prey in those which had eaten. Except for female *A. humilis*, which show fewer, smaller prey, yielding significantly less volume, there is not significantly less food volume in those with food in their stomachs. The late dry season difference appears to be attributable primarily to completely empty stomachs, expecially in smaller individuals. Whether this is really due to the decline or absence of food, or to some behavioral change can not be determined from this study.

Between size classes of both *A. humilis* and *A. limifrons*, S_t is significantly higher than S_l ($P<.05$ for both species, Mann-Whitney test for this and all other comparisons of indices). In comparisons between collecting periods (Table 5-29), both S_t and S_l are significantly lower than between classes ($P<.001$ for both for *A. humilis*, $P<.01$ for both for *A. limifrons*), and S_l and S_t are not significantly different between collecting periods for either species. It would seem, then, that the various size classes take prey that is more similar in both size and taxon to that of other size classes, than that of the large classes of one season compared to large classes of another season.

Niche overlap for prey taxa (L_t) is significantly higher than overlap for prey length (L_l) between size classes of both species (P<.001 for both). Also between collecting periods, L_t is significantly higher than L_1 for both *A. humilis* (P<.001) and *A. limifrons* (P<.01). L_t is higher because all sizes of both species use prey from several taxa more than proportional to the abundance of those taxa, regardless of season.

Prey size use, even though it varies by season and by anole size, is more closely proportional to the prey size abundance, thus L_1 is consistently lower than L_t. One would then expect intraspecies conflicts[1] more often over prey of like taxa than of like size.

7. Interspecies Comparisons

Often, as is true at Río Frío, the most obvious difference between the species of anoles in a complex assemblage is body size. As has been described above, adult anoles at Río Frío vary in size from the 35 mm, 1 g *A. humilis* to *A. biporcatus*, almost three times as long and twenty times as heavy. Sizes of anoles are given in Table 4-1, and relative head dimensions can be seen by comparison of figures 5-13 through 5-20. Given this wide disparity in predator size, it would not be unexpected to find parallel differences in prey size.

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[1] Conflict as used here, does not necessarily denote a struggle for a prey item, simply that the same item would be used by two lizards if they found it, whether lizards of different size classes, or the same size class in different seasons. Once a resource has been utilized (eaten, in this case) it is no longer available whether it was utilized in an earlier season or by a different sized congener.

Schoener (1968), Schoener and Gorman (1968) and Andrews (1971a) have all compared two or more species of *Anolis* and found that the large anoles tend to take large and small prey, while small anoles are restricted to small prey.

Río Frío anoles seem to follow the pattern described above. Table 5-26 and figures 5-21 and 5-25 show that, in general, as anole size increases, prey size increases. When the prey length distribution of large classes of each species are compared to those of other species, it can be seen that there is usually a significant difference, with the larger predator taking more large prey items.

Anolis lionotus is the major exception to the pattern of discrete prey size distributions. Prey sizes of male *A. lionotus* are not significantly different from those of any other species. Females differ only from *A. capito* females which had a sample size of only four items, three of which were over 15 mm long. If *A. lionotus* broadly overlaps all other species in prey size, there must be a reason. That reason can be found in the habitat preference of this species. *A. lionotus* is, in a sense, a solitary species. In its narrow streamside habitat it has no anole competitors. As a result, it seems to be advantageous for it to feed on a broad spectrum of prey, including more of the small, abundant prey species than its relatively large size would otherwise suggest.

A. pentaprion females are underrepresented in my collection, and few had prey in their stomachs. Those that did contained among their prey, several small beetles (primarily weevils of apparently different species). These items may be typical of the prey of that species, although the rest of the items and the prey of the males of *A. pentaprion* are primarily flies, bees, a few beetles and a few ants, all of slightly larger sizes. It is more likely that the one or two individuals that fed on those weevils, picked them off the recently cut trees, to which many small weevils were attracted. In all likelihood, if adequate samples were available, prey size of *A. pentaprion* of both sexes would be found to be larger than the three smallest species, and not significantly different from that of *A. lemurinus*.

If *A. lionotus* and female *A. pentaprion* are excepted, all comparisons where there is not a significant difference in prey size involve species in which there is little difference in lizard size. The three smallest species, *A. humilis, A. limifrons* and *A. carpenteri*, make up a trio, none of which differs from either of the others[1]. While this similarity in prey size might be expected to cause significant competition, this is probably largely alleviated by the vertical displacement of these species: *A. humilis* on the ground, *A. limifrons* at shrub, low trunk level, and *A. carpenteri* high in the trees.

Another instance of similar prey size is found in the similar sized *A. lemurinus* and *A. pentaprion*, one of which is found on trunks, the other in the crown. *A. biporcatus*, a trunk-crown inhabitat is only slightly larger than *A. capito*, a ground dwelling anole, and they are not significantly different in prey size distributions. The relationships between anole size, prey size and habitat are displayed in figure 5-26.

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[1] This assumes that the 21 small beetles from one and 19 small spiders from another female *A. limifrons* are either deleted or counted as a single item.

As pointed out in section 5-4, within each species there seems to be an almost linear increase in average prey length with increasing anole length. Schoener (1968) and Schoener and Gorman (1968) found this to be true in their South Bimini and Grenada anoles, and in addition, found the increase in average prey size to be greater for the larger species than for smaller species. Figure 5-27 shows this to be the case at Río Frío as well. Straight lines were fit to the same mean prey sizes used for figure 5-21 for the six species with adequate samples. The slopes of the lines (Table 5-25) generally increase as the size of the species increases, with the exception of *A. lionotus* which, as has been pointed out above, eats less large prey than expected. Correlation of slope with mean large class SVL is significant for females ($r=0.88$, $P_{(r=o)}<.05$) but not for males ($r=0.75$). If *A. lionotus* is not included, the correlation is greater for both sexes (females, $r=0.97$, $P<.01$; males $r=0.95$, $P<.05$).

Similarity and overlap indices were calculated for all possible combinations of species for both large males and large females (Tables 5-21 and 32). As might be expected, S_1 between species is significantly less than between different classes of the same species ($P<.05$, Mann-Whitney test).

Interspecies pairs are usually more different in size than are intraspecies pairs, as a consequence, they differ more in prey size. In contrast, L_1 is not significantly less between species than between classes. This is due to the high L_1's between species which are not markedly similar in prey size, but which do overlap at the least abundant, large-sized prey.

Although prey taxa are determined to some extent by prey size preferences (most orthoptera are large, most bark lice small, etc.), the availability of prey by taxa may be more influenced by habitat. It is not surprising then that S_t is lower for interspecies comparisons, which are more likely to also be inter-habitat comparisons, than for interclass comparisons ($P<.001$). Because all classes of many species feed heavily on the same, less abundant taxa, interclass S_t's are higher than S_t's between species, where there is less likelihood of their having the same prey taxa. Prey taxa of large males and females are summarized in figure 5-26.

Interspecies comparison of prey sizes between the large classes of the anoles is appropriate because those are the sizes which probably best represent the adaptation of the species. On the other hand, many interspecies prey conflicts must occur between the large class of one species and the small of another. Many of these possible interactions are worthy of investigation.

Not only would comparing each of the six or seven classes of each species with each class of all other species be extremely tedious[1], many of the comparisons would be of little interest. For example, comparing juvenile *A. humilis* with large female *A. biporcatus*, which are six times as long, 170 times as heavy and live in an entirely different place, would not be expected to yield particularly exciting results. The comparisons of this kind that would be of greatest value would be between similar-sized individuals of different species that share a common habitat.

To facilitate such comparisons, classes of males and females were combined, and juveniles of *A. humilis* and *A. limifrons* were combined with the small classes. Each species is, thus, separated into three classes: small, medium, and large. Each of these combined classes was then paired with classes of other species which had $\overline{SVL}$'s no more than about 15% greater than the $\overline{SVL}$ of the first. In a few cases, classes with larger differences were compared in order to compare at least one class of each species with one of each other species with which it shares a habitat, e.g. large *A. humilis* are compared with small *A. capito* even though they are about 30% larger, because both inhabit the ground-tree base habitat (See section III). The significance of differences in prey length distributions for these 28 pairs are given in table 5-34.

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[1] In addition to the 132 interclass comparisons and the 56 interspecies comparisons between large classes that have already been discussed, this would involve an additional 1037 pairs!

As one might expect, classes of similar sized anoles of different species do not usually have different prey distributions when the species are of different habitat preference. Five of eight such differences involve *A. lionotus*. As has been discussed above, *A. lionotus* takes a fairly wide spectrum of prey sizes, but feeds most heavily on prey that are smaller than might be expected for its size. As a result, small *A. lionotus* take significantly more small items than similar sized *A. humilis, A. limifrons* and *A. carpenteri*. Also, medium *A. lionotus* take fewer large items than the smaller small *A. capito* as do large *A. lionotus* compared to the slightly larger small *A. biporcatus*. Two other differences involve the flattened, twig-dwelling *A. pentaprion* which takes prey that is smaller than would be expected from its size probably in part because of its preference for small, flying insects that are more common in the tree crown. The final difference is between the very slim, twig-dwelling *A. carpenteri* and the stout, trunk-dwelling *A. lemurinus*. At similar SVL, *A. lemurinus* takes larger prey which might be expected from its general stockiness (Though the medium *A. lemurinus* are only 13.5% longer than the large *A. carpenteri*, they are 127% heavier.). Where the similar sized interspecies pairs share a common habitat, differences are more often significant, but, in many, size difference is greater.

Interspecies comparisons all tend to show that, on the whole, there is much less conflict for prey between species than there is between different classes of the same species. Prey length distributions are seldom different for intraspecies comparisons, but often different for interspecies pairs. There is greater similarity of both prey size and taxa within than between species and greater overlap of prey taxa within species. It appears then that an individual anole's closest food competitor, that is the other anole most likely to try to capture the same prey item, will be another member of the same species, not of another species.

8. Prey Utilization by All Anoles
or
Leaving No Stone Unturned

If the eight species of *Anolis* are the only members of a guild of diurnal, arboreal (or at least tree-associated), insectivorous, rain forest lizards at Río Frío, as has been suggested above, one might expect this group to have expanded to fill all available prey niches. In other words, we might expect that the entire anole fauna would utilize their arthropod prey in exact proportion to their availability. It appears that for both size and taxa they are close to this hypothesis, with some important differences.[1]

To consider prey utilization by the entire anole fauna, we first need a sample of anoles. While the 941 *Anolis* in my collection will be used, for best results we should have a sample in which not only each species, but each size class is represented in proportion to its actual abundance. In all likelihood, my collection does not meet this criterium, for several reasons. First, large, arboreal species were probably over-collected in the trees which had just been cut. Knowing that *A. humilis* and *A. limifrons* were common, I tended to ignore them while collecting in the trees. *A. humilis* and *A. limifrons* however, are over-represented because of the large samples collected in population quadrats, in which few other species were collected. *A. capito* is probably more common than my collection would indicate, but they were not found on the just-felled trees, and were collected only twice in quadrats. The proportion of *A. lionotus* is largely unrelated to the other species. That species was only found along streams, so to collect my series, I made a special trip once or twice each period to secure a sample. It was never found in quadrats or among the trees. Juvenile anoles, in addition to being harder to find and collect because they are smaller, seem to be less obvious in their movements and more prone to drop and freeze or hide. As a result, juveniles of all species are probably under-represented with the possible exception of *A. humilis* and *A. limifrons*, the samples of which are largely composed of quadrat samples in which all individuals were collected. Some of these deficiencies of my collection tend to cancel others, leaving a sample that may not be perfect, but is still of reasonable value for such a comparison. The size and taxonomic distributions of the 1912 prey items taken from the Río Frío anoles are listed in table 5-35.

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[1] To reiterate a point made earlier, any discussion of proportional prey utilization is, of course, dependant on the knowledge of prey availability which is incomplete, at best.

When the distribution of arthropods (Janzen and Schoener, 1968) and the distribution of anole prey items are plotted by length (Figure 5-28), both are obviously not normal, being skewed to the left. The long right tail of the distribution representing the larger items, is even more obvious in the anole prey than in the sweep sample arthropods. Such prey distributions are often assumed to be log normal distributions. Hespenheide (1971) found that, indeed, distributions of beetles from a variety of bird species were normal when lengths were transformed to a $\log_{10}$ of length. However, Schoener and Janzen (1968) tested the log distributions of several samples of insects, including that which is used here as prey abundance, and found them all to vary significantly from normality. They utilized a Chi-squared test (Bliss, 1967:144) utilizing the statistics g_1, a measure of skewness, and g_2, a measure of kurtosis. In most insect distribtuions, they found g_1's to be positive, implying a long right tail, and g_2's to be positive implying a curve that is too pointed.

Distributions of all prey items and all arthropod prey items were tested using the X^2 test of Bliss (1967), with the appropriate corrections for unequal classes (Table 5-36). Distributions of prey of all species combined, and of each species separately were found to be significantly non-normal with the exception of that of *A. pentaprion*. When distributions were transformed to $\log_{10}$ of prey length distributions, most were not significantly different from normal. The distributions for all species, all items and arthropods only, were both non-normal with the same positive g_1's and g_2's found by Schoener and Janzen (1968) for sweep samples. The log distribution of *A. limifrons* prey was also not normal, with positive g_1, too long a right tail, and positive g_2, too peaked, as a result of too many items close to the mean size. This was true for the prey of *A. limifrons* even if the 19 small spiders and 21 small beetles discussed earlier were deleted. The distribution of *A. pentaprion* was normal before transformation, thus transformed, it lost the normality. As a generalization then, prey of an anole species is log normally distributed. Yet the distribution of all prey items (or of all arthropod items) of all species is more like the sweep-sample distributions, long-right tailed and too peaked. There are differences however.

When cumulative frequency is plotted versus the $\log_{10}$ length (Figure 5-29) on normal probability paper, the line would be straight for a normal distribution (Hespenheide, 1971). Both the Janzen and Schoener (1968) sweep samples and the anole prey produce relatively straight lines, but they both still bend toward the right due to the long right tails. The really interesting point of this figure is, however, that the prey item line is set off to the right of the sweep sample line, indicating that the anoles select a still greater portion from the large size edge of the available insects. This difference is significant ($P<.001$, Kolmogorov-Smirnov test). That the anoles concentrate on the larger items, to the exclusion of the smallest items was also suggested by the preponderance of overlap (L_1) values in excess of 1.0.

It is possible that an under-representation of juveniles, leaves the distribution deficient in small prey items, but it is doubtful that the slight lack of juvenile lizards would make the difference obvious in figures 5-28 and 5-29. A much more reasonable hypothesis is that the other non-lizard competitors prey more and perhaps more efficiently, on arthropods of less than 2-3 mm in length. It would seem reasonable that these items would be most easily handled by most predatory insects, spiders and the numerous small frogs, primarily *Eleutherodactylus* spp. and *Dendrobates pumilio*, which are so common in the Caribbean lowland rain forest. Anoles would be more likely to derive a positive energy balance from predation on slightly larger, though slightly less abundant items.

When arthropod abundance by taxa (Table 5-1) is plotted with prey distribution in all *Anolis*, the arrays are again quite similar with a few major differences (Figure 5-30). If the distributions are compared with a Chi-squared, goodness-of-fit test, there is, of course, a significant difference ($X^2=4579.48$, $P<.001$).

The taxon with the most obvious difference is Formicidae, ants. *Anolis* at Río Frío rarely eat ants. The combined estimate of 44.66% ants available is probably conservative, yet only 6% of all anole prey items were ants. No species feeds on ants in nearly the proportion that they are available, the highest being *A. pentaprion* with 16.1% followed by *A. biporcatus* with 12.9%. These findings are in contrast to Schoener's (1968) report that one of four anoles on South Bimini, *A. distichus*, contained 75% to 91% ants, depending on the size class. Other mainland species are more similar to Río Frío anoles. Andrews (1971a) found from 4% to 24% ants in *A. polylepis*, depending on size class and season, and 10% in *A. capito*. Talbot (1979) reported 3% or 4% and 0% or 4% Hymenoptera, presumably mostly ants, in *A. humilis* and *A. limifrons*, depending on the sex, at a site about 10 km from Río Frío. Fleming and Hooker (1975) reported ants in 9% to 54% of the *A. cupreus* stomachs examined, but did not report ants as the number or percent of items.

If ants are left out of both the arthropod abundance and the prey distributions (Figure 5-31), there is a closer match. Chi-squared has been reduced to 2034.67 by leaving out ants, but this is of course still a significant difference ($P<.001$). The taxon adding the most to Chi-squared (1519 of 2035) with ants removed is Lepidoptera larvae. Where ants were avoided, caterpillars are preferentially selected. High proportions of Lepidoptera larvae were reported by Andrews (1971a) for *A. polylepis* and *A. capito*, by Fleming and Hooker (1975) for *A. cupreus* in the wet season. Talbot (1979) reported only

0% and 3% for *A. humilis* (10% at Río Frío) and 8% and 9% for *A. limifrons* (18% at Río Frío).

Anoles, then, tend to eat all that is available to them, just about as it is available. The exceptions are that they eat more large items (or less small) and too few ants (or more of the more desirable taxa). It should be noted that the lack of ants may be merely a reflection of the lack of small items, since most ants fit in the less than 2 mm group that is under-represented in all diets. It would be interesting to examine the stomach contents of the small frogs that compete with the anoles, to see if they feed largely on ants.

TABLE 5-1. Prey Availability by Lengths

LENGTH	PERCENT
0.0- 1.0	3.25
1.1- 2.0	16.42
2.1- 3.0	43.26
3.1- 4.0	11.80
4.1- 5.0	9.11
5.1- 6.0	6.43
6.1- 7.0	4.87
7.1- 8.0	1.94
8.1- 9.0	0.75
9.1-10.0	0.75
10.1-11.0	0.31
11.1-12.0	0.31
12.1-13.0	0.31
13.1-14.0	0.12
14.1-15.0	0.06
15.1-20.0	0.06
20.1-25.0	0.06
25.1-30.0	0.06
30.1-50.0	0.06
>50.0	0.06

SOURCE: Janzen and Schoener, 1968.

TABLE 5-2. Prey Availability by Taxa

Taxon	Percent
Orthoptera	6.66
Isoptera	1.10
Psocoptera	0.85
Hemiptera	2.20
Homoptera	4.39
Coleoptera: adults	11.97
Coleoptera: larvae	0.15
Lepidoptera: adults	0.22
Lepidoptera: larvae	0.44
Diptera: adults	6.46
Diptera: larvae	0.15
Hymenoptera: excluding ants	4.67
Hymenoptera: Formicidae	44.66
Miscellaneous Insect Pupae	0.15
Isopoda	1.84
Diplopoda and Chilopoda	1.17
Araneida	11.73
Chelonethida	0.15
Unidentified Arthropoda	0.15
Mollusca	0.15
Vertebrata	0.15
Miscellaneous	0.60[†]

SOURCE: Janzen and Schoener (1968) and Andrews (1971a), see text for details of combination.

[†] Includes Dermaptera (0.2%), Neuroptera (0.3%), Thysanura (0.7%).

TABLE 5-3. Lengths of Specimens Included in Each Size Class

CLASS	*humilis*	*limifrons*	*carpenteri*	*lemurinus*
LF†	35.76 (±0.21)	39.59 (±0.15)	41.50 (±0.42)	57.38 (±0.47)
	34.0-40.0 (49)	38.0-42.0 (72)	40.5-43.5 (7)	55.0-60.0 (13)
LM	33.22 (±0.14)	37.15 (±0.13)	36.50 (±0.41)	47.79 (±0.31)
	32.0-36.5 (53)	36.0-40.5 (72)	35.5-40.0 (11)	46.0-51.5 (24)
MF	30.76 (±0.42)	36.24 (±0.17)	37.30 (±1.07)	48.42 (±1.14)
	26.5-33.5 (35)	34.0-37.5 (41)	34.0-40.0 (5)	44.0-54.0 (12)
MM	29.42 (±0.34)	34.77 (±0.093)	34.57 (±0.17)	40.78 (±0.78)
	26.0-31.5 (30)	33.5-35.5 (50)	34.0-35.0 (7)	36.0-45.5 (20)
SF	23.20 (±0.27)	29.15 (±0.48)	30.21 (±0.83)	33.65 (±1.38)
	21.5-25.5 (22)	23.0-33.5 (43)	26.5-32.5 (7)	26.0-43.0 (13)
SM	23.08 (±0.30)	29.36 (±0.43)	27.94 (±1.53)	30.34 (±0.80)
	20.0-25.5 (24)	24.0-33.0 (48)	19.5-33.5 (9)	22.0-33.5 (22)
UJ	16.87 (±0.23)	20.30 (±0.34)		
	12.0-19.5 (39)	17.0-22.5 (27)		

TABLE 5-3. - extended

CLASS	*pentaprion*	*lionotus*	*capito*	*biporcatus*
LF	56.80 (±0.37)	58.58 (±0.58)	83.25 (±1.25)	90.63 (±0.80)
	56.0-58.0 (5)	56.0-62.5 (12)	82.0-87.0 (4)	87.5-93.5 (8)
LM	61.50 (±1.86)	65.11 (±1.20)	75.80 (±1.10)	88.75 (±0.32)
	58.0-66.5 (4)	59.5-73.0 (14)	73.5-79.5 (5)	87.0-90.0 (12)
MF	47.75 (±1.90)	50.54 (±1.01)	73.00 (±4.00)	85.00 (±0.27)
	43.0-51.5 (4)	45.5-55.5 (12)	69.0-77.0 (2)	84.5-86.0 (5)
MM	55.63 (±1.38)	52.08 (±1.43)	71.13 (±1.25)	84.12 (±0.51)
	51.0-56.0 (4)	44.0-57.5 (13)	67.5-73.0 (4)	80.5-86.0 (13)
SF	37.00 (±2.27)	36.33 (±1.66)	40.67 (±4.38)	77.55 (±3.23)
	29.5-42.5 (5)	26.0-42.0 (12)	32.5-47.5 (3)	50.0-84.0 (10)
SM	47.75 (±1.39)	31.07 (±1.23)	47.10 (±6.09)	67.13 (±3.95)
	44.0-50.5 (4)	25.5-41.0 (14)	33.0-63.0 (5)	35.5-79.0 (12)

NOTE: mean (±standard error) above, range (sample size) below

† long females (LF), long males (LM), medium females (MF), medium males (MM), small females (SF), small males (SM), unsexed juveniles (UJ); see text for definition of classes.

TABLE 5-4. Prey Taxa - *Anolis humilis*, All Periods

PREY TAXON	UNSEXED JUV.		SHORT ♂♂		SHORT ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	I[†]	V[Φ]	I	V	I	V	I	V	I	V
Orthoptera	3.85	4.29	19.61	28.57	12.82	25.83	8.00	7.94	9.47	29.55
Isoptera									5.26	1.65
Psocoptera	2.56	1.41					4.00	0.48	1.05	1.39
Hemiptera							2.00	0.79		
Homoptera	2.56	0.37	9.80	6.42	10.26	14.73	10.00	11.27	5.26	2.05
Coleoptera: adults	2.56	0.29	1.96	0.32	17.95	7.26	8.00	1.11	10.53	4.04
Coleoptera: larvae	5.13	3.19	3.92	0.51	5.13	10.66	8.00	10.05	3.16	0.89
Lepidoptera: adults			1.96	10.32	2.56	0.62			1.05	5.17
Lepidoptera: larvae	10.23	29.81	11.76	15.45	5.13	5.56	8.00	19.99	7.37	23.43
Diptera: adults	12.82	6.78			7.69	1.09	6.00	8.97	4.21	1.23
Diptera: larvae	1.28	2.33	1.96	0.70	2.56	0.07	2.00	0.17		
Hymen.: excl. ants									1.05	0.01
Hymen.: Formicidae	7.69	2.94	1.96	0.05			8.00	2.86	4.21	2.89
Misc. Insect Pupae										
Isopoda	11.54	14.84	17.65	14.84	12.82	17.71	12.00	17.86	25.26	12.74
Dipolpoda/Chilopoda			1.96	4.09					2.11	0.59
Araneida	20.51	32.57	27.45	18.72	20.51	16.18	22.00	18.46	18.95	14.26
Chelonethida										
Unident. Arthropoda	1.28	1.02			2.56	0.27	2.00	0.04		
Mollusca										
Vertebrata										
Miscellaneous	8.97[∇]	0.17							1.05[Ψ]	0.10
Total Number, Volume	78	180.46	51	457.38	39	256.69	50	428.07	95	992.15

TABLE 5-4 - extended

PREY TAXON	LONG ♂♂		LONG ♀♀		ALL LONG		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	7.79	27.51	6.99	19.35	7.27	22.05	8.82	22.42
Isoptera	6.49	2.37	2.80	0.38	4.09	1.04	2.63	0.90
Psocoptera	2.60	0.46			0.91	0.15	1.31	0.41
Hemiptera	2.60	0.74			0.91	0.25	0.56	0.21
Homoptera	3.90	4.57	3.50	4.70	3.64	4.66	5.44	5.15
Coleoptera: adults	16.88	3.36	9.79	3.12	12.27	3.20	9.57	3.05
Coleoptera: larvae	2.60	2.26	4.90	0.47	4.09	1.06	4.50	2.15
Lepidoptera: adults	1.30	0.19	1.40	3.09	1.36	2.14	1.13	3.01
Lepidoptera: larvae	12.99	30.28	7.69	14.30	9.55	19.59	10.32	19.65
Diptera: adults	9.09	4.04	4.90	3.60	6.36	3.74	6.38	3.38
Diptera: larvae			6.29	3.07	4.09	2.05	2.44	1.37
Hymen.: excl. ants							0.19	0.00
Hymen.: Formicidae	10.39	7.69	8.39	1.10	9.09	3.28	6.57	2.77
Misc. Insect Pupae	1.30	0.51	3.50	4.77	2.73	3.36	1.13	2.01
Isopoda	7.79	5.84	14.69	14.61	12.27	11.71	15.01	12.96
Diplopoda/Chilopoda			4.90	3.75	3.18	2.51	1.88	1.93
Araneida	12.99	10.08	18.88	23.44	16.82	19.02	19.51	18.43
Chelonethida	1.30	0.09			0.45	0.03	0.19	0.02
Unident. Arthropoda			1.40	0.27	0.91	0.18	0.94	0.15
Mollusca								
Vertebrata								
Miscellaneous							1.50	0.02
Total Number, Volume	77	1143.59	143	2258.79	220	3402.38	533	5717.13

†Percentage of number of items.

ΦPercentage of volume (mm^3) of items.

∇Collembola (6, 0.31 mm^3), Thysanura (1, 0.01 mm^3).

ΨTick (1, 1.02 mm^3).

TABLE 5-5. Prey Taxa - *Anolis limifrons*, All Periods

PREY TAXON	UNSEXED JUV.		SHORT ♂♂		SHORT ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	$I^{\dagger}$	V^{Φ}	I	V	I	V	I	V	I	V
Orthoptera	10.53	26.26	7.69	21.66	8.96	15.79	6.25	4.37	8.57	23.74
Isoptera										
Psocoptera			1.28	0.22	13.43	3.79			1.90	0.25
Hemiptera			1.28	0.46					1.90	0.61
Homoptera	10.53	9.56	7.69	8.52	13.43	9.07	10.94	15.23	16.19	10.22
Coleoptera: adults	2.63	2.02	11.54	4.30	11.94	4.84	25.00	8.25	21.90	5.07
Coleoptera: larvae			2.56	0.42			3.13	1.45	1.90	0.62
Lepidoptera: adults			2.56	0.87	1.49	10.02				
Lepidoptera: larvae	2.63	43.47	11.54	27.63	7.46	24.32	4.69	10.39	3.81	13.54
Diptera: adults	36.84	6.42	15.38	4.88	14.93	9.41	18.75	21.58	10.48	8.67
Diptera: larvae			2.56	1.47	1.49	4.46	3.13	3.85	1.90	0.93
Hymen.: excl. ants			1.28	0.15			1.56	1.05		
Hymen.: Formicidae			8.97	1.05					2.86	1.30
Misc. Insect Pupae									0.95	1.92
Isopoda	5.26	3.41	5.13	15.44	2.99	2.16	4.69	4.60	9.52	14.13
Diplopoda/Chilopoda	2.63	0.34			1.49	0.16			2.86	0.41
Araneida	26.32	8.51	17.95	11.75	20.90	15.92	18.75	28.48	12.38	9.52
Chelonethida					1.49	0.08	3.13	0.76		
Unident. Arthropoda			1.28	0.07					2.86	1.33
Mollusca										
Vertebrata										
Miscellaneous	2.63^{∇}	0.10	1.28^{Ψ}	1.10						
Total Number, Volume	38	172.93	78	471.80	67	402.20	64	518.91	105	1291.50

TABLE 5-5 - extended

PREY TAXON	LONG ♂♂		LONG ♀♀		ALL LONG		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	8.08	28.93	7.80	34.76	7.89	33.12	8.08	28.39
Isoptera								
Psocoptera	1.01	0.28			0.33	0.08	1.98	0.34
Hemiptera	2.02	0.77	0.98	0.12	1.32	0.30	1.07	0.32
Homoptera	14.14	8.15	12.20	9.56	12.83	9.16	12.50	9.82
Coleoptera: adults	20.20	3.94	21.46	5.44	21.05	5.02	18.45	5.14
Coleoptera: larvae	2.02	2.69	1.46	8.57	1.64	6.93	1.68	4.14
Lepidoptera: adults	1.01	0.78	0.98	3.49	0.99	2.73	0.91	2.21
Lepidoptera: larvae	7.07	19.32	5.37	16.52	5.92	17.30	6.10	17.88
Diptera: adults	8.08	3.18	9.76	3.10	9.21	3.12	13.26	6.31
Diptera: larvae			0.49	0.14	0.33	0.10	1.22	0.93
Hymen.: excl. ants	1.01	1.37	0.49	0.11	0.66	0.46	0.61	0.35
Hymen.: Formicidae	5.05	0.44	2.44	0.64	3.29	0.58	3.05	0.66
Misc. Insect Pupae							0.15	0.38
Isopoda	2.02	0.91	3.90	2.58	3.29	2.11	4.73	5.72
Diplopoda/Chilopoda			0.98	1.04	0.66	0.75	1.07	0.52
Araneida	26.26	27.55	30.73	13.50	29.28	17.43	23.17	15.99
Chelonethida	1.01	0157			0.33	0.16	0.61	0.15
Unident. Arthropoda			0.49	0.00	0.33	0.00	0.76	0.27
Mollusca								
Vertebrata								
Miscellaneous	1.01[Θ]	1.13	0.49[T]	0.43	0.66	0.63	0.61	0.43
Total Number, Volume	99	1012.05	205	2601.43	304	3613.48	656	6470.82

[†] Percentage of number of items.

[Φ] Percentage of volume (mm^3) of items.

[∇] Collembola (1, 0.18 mm^3).

[Ψ] Dermaptera (1, 5.20 mm^3).

[Θ] Dermaptera (1, 11.44 mm^3).

[T] Thysanura (1, 11.20 mm^3).

TABLE 5-6. Prey Taxa - *Anolis carpenteri*, All Periods

PREY TAXON	SMALL ♂♂		SMALL ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	I[†]	V[Φ]	I	V	I	V	I	V
Orthoptera					14.29	30.40		
Isoptera								
Psocoptera								
Hemiptera			7.69	7.46			8.33	3.50
Homoptera	9.09	16.14	30.77	66.83	14.29	3.45	16.77	47.77
Coleoptera: adults	9.09	9.14	7.69	0.90	14.29	11.86	41.67	11.07
Coleoptera: larvae			7.69	6.30				
Lepidoptera: adults								
Lepidoptera: larvae	4.55	10.40						
Diptera: adults	9.09	7.38	7.69	3.15	14.29	17.45		
Diptera: larvae								
Hymen.: excl. ants							8.33	0.59
Hymen.: Formicidae								
Misc. Insect Pupae								
Isopoda								
Diplopoda/Chilopoda								
Araneida	36.36	37.63	23.08	11.92	28.57	32.36	16.67	35.11
Chelonethida			7.69	1.15			8.33	1.97
Unident. Arthropoda								
Mollusca	31.82	19.32	7.69	2.30	7.14	2.69		
Vertebrata								
Miscellaneous					7.14[▽]	1.79		
Total Number, Volume	22	52.86	13	140.73	14	107.28	12	156.47

TABLE 5-6 - extended

PREY TAXON	LARGE ♂♂		LARGE ♀♀		ALL LARGE		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	7.41	25.74	17.39	21.70	12.00	23.38	7.21	15.23
Isoptera								
Psocoptera								
Hemiptera							1.80	1.75
Homoptera			21.74	50.01	10.00	29.16	13.51	34.38
Coleoptera: adults	25.93	14.82	17.39	7.52	22.00	10.56	18.92	9.23
Coleoptera: larvae			4.35	3.51	2.00	2.05	1.80	1.99
Lepidoptera: adults			4.35	0.12	2.00	0.07	0.90	0.04
Lepidoptera: larvae							0.90	0.60
Diptera: adults	7.41	12.11	13.04	3.62	10.00	7.16	9.01	6.53
Diptera: larvae								
Hymen.: excl. ants	7.41	2.76			4.00	1.15	2.70	0.68
Hymen.: Formicidae	7.41	13.06	4.35	2.22	6.00	6.74	2.70	3.36
Misc. Insect Pupae								
Isopoda	7.41	4.59	8.70	7.22	8.00	6.12	3.60	3.05
Diplopoda/Chilopoda								
Araneida	33.33	22.61	8.70	4.08	22.00	13.48	25.23	20.57
Chelonethida							1.80	0.52
Unident. Arthropoda	3.70	0.32			2.00	0.13	0.90	0.07
Mollusca							8.11	1.79
Vertebrata								
Miscellaneous							0.90	0.21
Total Number, Volume	27	189.65	23	265.19	50	454.84	111	912.18

[†] Percentage of number of items.

[Φ] Percentage of volume (mm^3) of items.

[∇] Dermaptera (1, 1.92 mm^3).

TABLE 5-7. Prey - *Anolis lemurinus*, All Periods

PREY TAXA	SMALL ♂♂		SMALL ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	I†	V$^{\Phi}$	I	V	I	V	I	V
Orthoptera	5.56	34.28	11.11	32.56	11.63	16.41	23.81	37.88
Isoptera								
Psocoptera	30.56	0.35						
Hemiptera	2.78	0.70	3.70	0.07				
Homoptera	5.56	11.73	3.70	0.13	4.65	0.93	4.76	0.82
Coleoptera: adults	9.72	4.15	14.81	3.82	16.28	3.35	14.29	1.86
Coleoptera: larvae	4.17	5.45	7.41	0.19	11.63	5.38		
Lepidoptera: adults								
Lepidoptera: larvae	6.94	16.04	11.11	46.84	9.30	22.07	23.81	38.07
Diptera: adults	4.17	0179	11.11	2.67				
Diptera: larvae							4.76	11.89
Hymen.: excl. ants			3.70	0.33				
Hymen.: Formicidae	5.56	5.91	3.70	4.48	4.65	1.49		
Misc. Insect Pupae					4.65	4.29		
Isopoda	4.17	2.33			4.65	0.77		
Diplopoda/Chilopoda								
Araneida	18.06	17.56	25.93	8.62	27.91	44.25	19.05	7.62
Chelonethida	1.39	0.23						
Unident. Arthropoda	1.39	0.48						
Mollusca			3.70	0.29	4.65	1.06	9.02	1.85
Vertebrata								
Miscellaneous								
Total Number, Volume	72	692.48	27	697.05	43	1397.07	21	2002.78

TABLE 5-7 - extended

PREY TAXON	LARGE ♂♂		LARGE ♀♀		ALL LARGE		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	16.67	37.98	17.14	61.00	16.88	55.09	12.50	42.70
Isoptera								
Psocoptera							9.17	0.03
Hemiptera			5.71	1.06	2.60	0.78	2.08	0.45
Homoptera	7.14	13.22			3.90	3.39	4.58	2.86
Coleoptera: adults	23.81	8.35	31.43	4.48	27.27	5.47	17.50	4.19
Coleoptera: larvae	2.38	0.41	2.86	0.34	2.60	0.36	5.00	1.37
Lepidoptera: adults			2.86	0.07	1.30	0.05	0.42	0.03
Lepidoptera: larvae	7.14	9.62	11.43	11.14	9.09	10.75	10.00	21.12
Diptera: adults							2.50	0.25
Diptera: larvae	2.38	0.34			1.30	0.09	0.83	2.53
Hymen.: excl. ants							0.42	0.02
Hymen.: Formicidae	28.57	18.08			15.58	4.64	7.92	3.29
Misc. Insect Pupae			2.86	0.28	1.30	0.21	1.25	0.73
Isopoda							2.08	0.28
Diplopoda/Chilopoda	2.38	5.21			1.30	1.34	0.42	0.67
Araneida	9.52	6.79	17.14	10.35	12.99	9.44	19.17	14.66
Chelonethida							0.42	0.02
Unident. Arthropoda							0.42	0.03
Mollusca			2.86	0.10	1.30	0.08	2.50	0.60
Vertebrata								
Miscellaneous			5.71[∇]	11.18	2.60	8.31	0.83	4.15
Total Number, Volume	42	1228.61	35	3556.70	77	4785.31	240	9574.69

[†] Percentage of number of items.

[Φ] Percentage of volume (mm^3) of items.

[∇] Dermaptera (1, 7.70 mm^3), Solpugida (1, 390.00 mm^3).

TABLE 5-8. Prey Taxa - *Anolis pentaprion*, All Periods

PREY TAXON	SMALL ♂♂		SMALL ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	I[†]	V[Φ]	I	V	I	V	I	V
Orthoptera								
Isoptera								
Psocoptera								
Hemiptera			16.67	15.52				
Homoptera								
Coleoptera: adults			50.00	48.06	42.86	41.05	20.00	1.61
Coleoptera: larvae								
Lepidoptera: adults								
Lepidoptera: larvae								
Diptera: adults	100.0	100.0	16.67	30.22			20.00	12.54
Diptera: larvae								
Hymen.: excl. ants								
Hymen.: Formicidae					28.57	41.39	40.00	15.49
Misc. Insect Pupae								
Isopoda								
Diplopoda/Chilopoda								
Araneida			16.67	6.19	28.57	17.56	20.00	70.36
Chelonethida								
Unident. Arthropoda								
Mollusca								
Vertebrata								
Miscellaneous								
Total Number, Volume	6	116.44	6	26.80	14	110.26	5	74.62

TABLE 5-8 - extended

PREY TAXON	LARGE ♂♂		LARGE ♀♀		ALL LARGE		ALL	
	I	V	I	V	I	V	I	V
Orthoptera								
Isoptera								
Psocoptera								
Hemiptera							1.79	0.65
Homoptera								
Coleoptera: adults	22.22	29.23	56.25	57.75	44.00	45.29	37.50	31.42
Coleoptera: larvae								
Lepidoptera: adults	11.11	17.41			4.00	7.61	1.79	3.73
Lepidoptera: larvae								
Diptera: adults	55.56	49.45	12.50	15.03	28.00	30.07	26.79	35.54
Diptera: larvae								
Hymen.: excl. ants			18.75	14.90	12.00	8.39	5.36	4.11
Hymen.: Formicidae	11.11	3.91	12.50	12.32	12.00	8.64	16.07	13.13
Misc. Insect Pupae								
Isopoda								
Diplopoda/Chilopoda								
Araneida							10.71	11.42
Chelonethida								
Unident. Arthropoda								
Mollusca								
Vertebrata								
Miscellaneous								
Total Number, Volume	9	137.85	16	177.61	25	315.46	56	643.58

†Percentage of number of items.

ΦPercentage of volume (mm^3) of items.

TABLE 5-9. Prey Taxa - *Anolis lionotus*, All Periods

PREY TAXON	SMALL ♂♂		SMALL ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	I†	VΦ	I	V	I	V	I	V
Orthoptera	2.78	4.72			5.00	0.90	6.25	14.82
Isoptera								
Psocoptera								
Hemiptera					10.00	1.22		
Homoptera	2.78	9.58	9.09	3.60				
Coleoptera: adults	11.11	2.65	9.09	1.21	30.00	4.05	6.25	0.87
Coleoptera: larvae	2.78	2.04	9.09	1.25				
Lepidoptera: adults								
Lepidoptera: larvae	25.00	68.08	9.09	32.17	5.00	7.81	37.50	2.08
Diptera: adults	16.67	2.84	27.27	54.27	10.00	43.88		
Diptera: larvae			9.09	1.99			43.75	81.95
Hymen.: excl. ants	5.56	0.42					6.25	0.27
Hymen.: Formicidae			9.09	0.65	10.00	0.19		
Misc. Insect Pupae	2.78	6.63						
Isopoda			9.09	4.63				
Diplopoda/Chilopoda								
Araneida	19.44	1.73	9.09	0.24	25.00	37.93		
Chelonethida								
Unident. Arthropoda								
Mollusca	11.11	1.30						
Vertebrata								
Miscellaneous					5.00	4.02∇		
Total Number, Volume	36	379.85	11	135.96	20	503.37	16	829.01

TABLE 5-9 - extended

PREY TAXON	LARGE ♂♂		LARGE ♀♀		ALL LARGE		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	11.11	42.53	5.56	11.42	7.41	22.69	4.55	12.86
Isoptera								
Psocoptera								
Hemiptera	11.11	3.52			3.70	1.28	2.73	0.65
Homoptera							1.82	1.48
Coleoptera: adults	22.22	3.38			7.41	1.22	12.73	1.82
Coleoptera: larvae			5.56	1.51	3.70	0.97	2.73	0.66
Lepidoptera: adults								
Lepidoptera: larvae	22.22	43.66	16.67	27.79	18.52	30.99	20.00	23.32
Diptera: adults	22.22	2.51	11.11	0.58	14.81	1.28	13.64	11.38
Diptera: larvae			5.56	36.80	3.70	23.47	8.18	32.38
Hymen.: excl. ants			11.11	0.89	7.41	0.57	4.55	0.33
Hymen.: Formicidae			11.11	11.40	7.41	7.27	4.55	2.52
Misc. Insect Pupae							0.91	0.90
Isopoda			16.67	6.84	11.11	4.36	3.64	1.70
Diplopoda/Chilopoda								
Araneida			16.67	6.77	11.11	4.32	14.55	8.55
Chelonethida								
Unident. Arthropoda								
Mollusca							3.65	0.18
Vertebrata								
Miscellaneous	11.11	4.40[Ψ]			3.70	1.59	1.82	1.26
Total Number, Volume	9	340.67	18	599.94	27	940.61	110	2788.80

[†] Percentage of number of items.

[Φ] Percentage of volume (mm^3) of items.

[∇] Plecoptera (1, 20.24 mm^3).

[Ψ] Odonata (1, 14.98 mm^3).

TABLE 5-10. Prey Taxa - *Anolis capito*, All Periods

PREY TAXON	SMALL ♂♂		SMALL ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	$I^{\dagger}$	V^{Φ}	I	V	I	V	I	V
Orthoptera	12.50	3.66	50.00	78.13			100.0	100.0
Isoptera								
Psocoptera								
Hemiptera								
Homoptera								
Coleoptera: adults	12.50	0.37						
Coleoptera: larvae	12.50	52.06						
Lepidoptera: adults	12.50	8.79						
Lepidoptera: larvae								
Diptera: adults								
Diptera: larvae								
Hymen.: excl. ants								
Hymen.: Formicidae	12.50	4.37						
Misc. Insect Pupae								
Isopoda	25.00	7.88						
Diplopoda/Chilopoda								
Araneida			50.00	21.88				
Chelonethida								
Unident. Arthropoda								
Mollusca								
Vertebrata								
Miscellaneous	12.50	22.87^{∇}						
Total Number, Volume	8	710.66	2	38.40	0		1	44.80

TABLE 5-10 - extended

PREY TAXON	LARGE ♂♂		LARGE ♀♀		ALL LARGE		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	40.00	79.59	50.00	59.59	44.44	70.81	35.00	60.40
Isoptera								
Psocoptera								
Hemiptera								
Homoptera								
Coleoptera: adults			25.00	0.42	11.11	0.19	10.00	0.21
Coleoptera: larvae							5.00	8.35
Lepidoptera: adults							5.00	1.41
Lepidoptera: larvae	40.00	19.67	25.00	39.98	33.33	28.59	15.00	23.46
Diptera: adults								
Diptera: larvae								
Hymen.: excl. ants								
Hymen.: Formicidae							5.00	0.70
Misc. Insect Pupae								
Isopoda							10.00	1.26
Diplopoda/Chilopoda								
Araneida	20.00	0.74			11.11	0.41	10.00	0.53
Chelonethida								
Unident. Arthropoda								
Mollusca								
Vertebrata								
Miscellaneous							5.00	3.67
Total Number, Volume	5	2040.11	4	1596.78	9	3636.89	20	4430.75

†Percentage of number of items.

ΦPercentage of volume (mm^3) of items.

∇Annelida (1, 162.50 mm^3).

TABLE 5-11. Prey Taxa - *Anolis biporcatus*, All Periods

PREY TAXON	SMALL ♂♂		SMALL ♀♀		MEDIUM ♂♂		MEDIUM ♀♀	
	I[†]	V[Φ]	I	V	I	V	I	V
Orthoptera	4.76	6.09	19.35	43.70	13.64	28.65	3.23	3.77
Isoptera								
Psocoptera			3.23	0.13				
Hemiptera	9.52	8.67	6.45	10.22	4.55	6.88	3.23	1.87
Homoptera	4.76	0.78	3.23	0.66	2.27	0.98		
Coleoptera: adults	52.38	21.03	35.48	19.83	45.45	30.54	45.16	21.55
Coleoptera: larvae					4.55	3.52		
Lepidoptera: adults	4.76	20.05						
Lepidoptera: larvae			3.23	15.61	4.55	6.92	25.81	27.21
Diptera: adults			3.23	0.02	2.27	3.41	3.23	2.91
Diptera: larvae								
Hymenop.: excl. ants			9.68	4.79				
Hymenop.: Formicidae					15.91	4.29	6.45	0.68
Misc. Insect Pupae								
Isopoda			3.23	0.57				
Diplopoda/Chilopoda			3.23	1.09				
Araneida	14.29	17.28	3.23	0.59	4.55	0.45		
Chelonethida			3.23	0.08				
Unident. Arthropoda								
Mollusca			3.23	2.73				
Vertebrata	9.52	26.10			2.27	14.37	9.68	42.50
Miscellaneous							3.23	0.50[▽]
Total Number, Volume	21	2872.70	31	2854.32	44	4696.28	31	5497.18

TABLE 5-11 - extended

PREY TAXON	LARGE ♂♂		LARGE ♀♀		ALL LARGE		ALL	
	I	V	I	V	I	V	I	V
Orthoptera	19.44	48.85	13.04	49.45	16.95	49.20	12.90	32.64
Isoptera								
Psocoptera							0.54	0.01
Hemiptera	11.11	11.55			6.78	4.73	5.91	5.46
Homoptera							1.61	0.30
Coleoptera: adults	25.00	8.87	26.09	8.03	25.42	8.37	38.17	16.75
Coleoptera: larvae							1.08	0.56
Lepidoptera: adults	2.78	7.96			1.69	3.26	1.08	3.46
Lepidoptera: larvae	5.56	9.87	13.04	25.83	8.47	19.29	8.60	16.36
Diptera: adults							1.61	1.09
Diptera: larvae								
Hymenop.: excl. ants	5.56	3.37			3.39	1.38	2.69	1.10
Hymenop.: Formicidae	19.44	4.83	34.78	1.40	25.42	2.81	12.90	2.10
Misc. Insect Pupae								
Isopoda							0.54	0.06
Diplopoda/Chilopoda							0.54	0.11
Araneida	11.11	4.70	4.35	0.31	8.47	2.11	5.91	2.79
Chelonethida							0.54	0.01
Unident. Arthropoda								
Mollusca							0.54	0.27
Vertebrata			4.35	10.24	1.69	6.05	3.76	15.59
Miscellaneous			4.35	4.73[Ψ]	1.69	2.80	1.08	1.37
Total Number, Volume	36	5493.72	23	7919.79	59	13413.51	186	29333.99

[†] Percentage of number of items.

[Φ] Percentage of volume (mm^3) of items.

[∇] Thysanura (1, 27.46 mm^3).

[Ψ] Odonata (1, 375.00 mm^3).

TABLE 5-12. Prey Size - *Anolis humilis*, All Periods

SIZE CLASS (mm)	JUVENILES	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀
0 - 1.0[†]	16.67	1.96			1.05
1.1- 2.0	34.62	15.69	15.38	16.00	15.79
2.1- 3.0	21.79	21.57	41.03	24.00	28.42
3.1- 4.0	10.26	17.65	15.38	24.00	23.16
4.1- 5.0	6.41	19.61	12.82	8.00	9.47
5.1- 6.0	7.62	7.84	5.13	8.00	7.37
6.1- 7.0	1.28	5.88	5.13	6.00	3.16
7.1- 8.0			2.56		2.11
8.1- 9.0	1.28	3.92		4.00	4.21
9.1-10.0				2.00	1.05
10.1-11.0				4.00	1.05
11.1-12.0		1.96	2.56		3.16
12.1-13.0		1.96		2.00	
13.1-14.0					
14.1-15.0		1.96			
15.1-20.0					
20.1-25.0					
25.1-30.0					
30.1-50.0					
>50.0					

[†] Percentage of number of items.

TABLE 5-12 - extended

LONG ♂♂	LONG ♀♀	ALL LONG	ALL
	1.40	0.91	3.19
12.99	9.09	10.45	16.32
29.87	23.08	25.45	26.08
18.18	17.48	17.73	18.01
6.49	18.88	14.55	12.20
7.79	7.69	7.73	7.50
5.19	2.80	3.64	3.75
3.90	2.10	2.73	1.69
2.60	7.69	5.91	4.13
5.19	2.80	3.64	1.88
1.30	2.10	1.82	1.31
3.90	1.40	2.27	2.06
	1.40	0.91	0.56
	0.70	0.45	0.38
	0.70	0.45	0.38
2.60	0.70	1.36	0.56

TABLE 5-13. Prey Size - *Anolis limifrons*, All Periods

SIZE CLASS (mm)	JUVENILES	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀
0 - 1.0[†]					0.95
1.1- 2.0	34.21	20.51	16.42	12.50	13.33
2.1- 3.0	39.47	20.51	35.82	29.69	14.29
3.1- 4.0	10.53	23.08	23.88	26.56	31.43
4.1- 5.0	10.53	12.82	5.97	12.50	14.29
5.1- 6.0		7.69	4.48	6.25	8.57
6.1- 7.0	2.63	5.13	7.46	6.25	4.79
7.1- 8.0		2.56	2.99	3.13	5.71
8.1- 9.0		2.56		1.56	1.90
9.1-10.0		2.56	1.49		0.95
10.1-11.0					1.90
11.1-12.0	2.63	1.28		1.56	
12.1-13.0		1.28	1.49		
13.1-14.0					0.95
14.1-15.0					
15.1-20.0					0.95
20.1-25.0					
25.1-30.0					
30.1-50.0					
>50.0					

[†] Percentage of number of items.

TABLE 5-13 - extended

LONG ♂♂	LONG ♀♀	ALL LONG	ALL
1.01	0.98	0.99	0.61
9.09	11.71	10.86	14.48
33.33	37.07	35.86	30.18
23.23	16.59	18.75	22.10
8.08	11.71	10.53	11.13
7.07	4.88	5.59	5.95
5.05	2.43	3.62	4.57
3.03	3.41	3.29	3.35
3.03	2.44	2.63	1.98
3.03	0.98	1.64	1.37
1.01	0.49	0.66	0.61
	1.46	0.99	0.91
	1.46	0.99	0.76
			0.15
2.02	2.44	2.30	1.07
1.01	0.98	0.99	0.61
	0.49	0.33	0.15

TABLE 5-14. Prey Size - *Anolis carpenteri*, All Periods

SIZE CLASS (mm)	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀	LONG ♂♂	LONG ♀♀	ALL LONG	ALL
0 - 1.0[†]	4.55							0.90
1.1- 2.0	45.45	7.69	14.29		3.70	4.35	4.0	13.51
2.1- 3.0	22.73	38.46	35.71	33.33	29.63	8.70	20.0	26.13
3.1- 4.0	13.64	30.77	7.14	33.33	33.33	34.78	34.0	26.13
4.1- 5.0	9.09		14.29	16.67	18.52	17.39	18.0	13.51
5.1- 6.0	4.55		14.29		3.70	13.04	8.0	6.31
6.1- 7.0		7.64	7.14	8.33	7.41	8.70	8.0	6.31
7.1- 8.0			7.14		3.70	4.35	4.0	2.70
8.1- 9.0		15.38		8.33				2.70
9.1-10.0						8.70	4.0	1.80
10.1-11.0								
11.1-12.0								
12.1-13.0								
13.1-14.0								
14.1-15.0								
15.1-20.0								
20.1-25.0								
25.1-30.0								
30.1-50.0								
>50.0								

[†] Percentage of number of items.

TABLE 5-15. Prey Size - *Anolis lemurinus*, All Periods

SIZE CLASS (mm)	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀	LONG ♂♂	LONG ♀♀	ALL LONG	ALL
0 - 1.0[†]								
1.1- 2.0	37.50	18.52	6.98		4.76	14.29	9.09	17.83
2.1- 3.0	16.67	18.52	13.95	9.52	2.38	5.71	3.90	12.18
3.1- 4.0	19.44	14.81	18.60	14.29	16.67	11.43	14.29	16.52
4.1- 5.0	1.39	22.22	9.30	4.76	16.67	11.43	14.29	9.57
5.1- 6.0	9.72	3.70	9.30	19.05	7.14	8.57	7.79	9.57
6.1- 7.0	5.56		11.63		21.43	5.71	14.29	8.70
7.1- 8.0	2.78	7.41	13.95	9.52	9.52	5.71	7.79	7.83
8.1- 9.0			4.65		14.29	14.29	14.29	4.35
9.1-10.0	2.78			4.76				1.30
10.1-11.0	1.39		2.33					0.87
11.1-12.0	1.39	3.70	2.33	4.76		5.71	2.60	2.17
12.1-13.0	1.39	3.70	2.33	9.52		5.71	2.60	3.04
13.1-14.0				4.76		2.86	1.30	0.43
14.1-15.0		3.70	2.33	9.52				1.74
15.1-20.0			2.33		4.76	2.86	3.90	1.30
20.1-25.0		3.70		4.76	2.38	2.86	2.60	1.74
25.1-30.0				4.76		2.86	1.30	0.87
30.1-50.0								
>50.0								

[†] Percentage of number of items.

TABLE 5-16. Prey Size - *Anolis pentaprion*, All Periods

SIZE CLASS (mm)	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀	LONG ♂♂	LONG ♀♀	ALL LONG	ALL
0 - 1.0[†]								
1.1- 2.0		16.67		20.00		6.25	4.00	5.36
2.1- 3.0		33.33	21.43	20.00		18.75	12.00	16.07
3.1- 4.0		33.33	28.57			12.50	8.00	14.29
4.1- 5.0		16.67	28.57		22.22	37.50	32.00	23.21
5.1- 6.0	83.33		7.14	20.00	55.56	18.75	32.00	26.79
6.1- 7.0			14.29	40.00	22.22		8.00	10.71
7.1- 8.0						6.25	4.00	1.79
8.1- 9.0	16.67							1.79
9.1-10.0								
10.1-11.0								
11.1-12.0								
12.1-13.0								
13.1-14.0								
14.1-15.0								
15.0-20.0								
20.1-25.0								
25.1-30.0								
30.1-50.0								
>50.0								

[†] Percentage of number of items.

TABLE 5-17. Prey Size - *Anolis lionotus*, All Periods

SIZE CLASS (mm)	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀	LONG ♂♂	LONG ♀♀	ALL LONG	ALL
0 - 1.0[†]								
1.1- 2.0	8.33	9.09	5.00					4.55
2.1- 3.0	47.22	9.09	15.00		11.11	11.11	11.11	21.82
3.1- 4.0	5.56	18.18	10.00	6.25		16.67	11.11	9.09
4.1- 5.0	8.33	18.18	15.00	6.25	22.22	5.56	11.11	10.91
5.1- 6.0	11.11		15.00	43.75	22.22	11.11	14.81	16.36
6.1- 7.0			10.00			11.11	7.41	3.64
7.1- 8.0	5.56	9.09	10.00			5.56	3.70	5.45
8.1- 9.0	2.78	27.27	5.00	6.25		5.56	3.70	6.36
9.1-10.0			5.00	12.50		5.56	3.70	3.64
10.1-11.0	2.78				11.11		3.70	1.82
11.1-12.0			5.00		11.11	5.56	7.41	2.73
12.1-13.0	2.78			6.25	11.11	11.11	11.11	4.55
13.1-14.0	2.78			18.75				3.64
14.1-15.0		9.09	5.00			11.11	7.41	3.64
15.1-20.0								
20.1-25.0	2.78				11.11		3.70	1.82
25.1-30.0								
30.1-50.0								
>50.0								

[†] Percentage of number of items.

TABLE 5-18. Prey Size - *Anolis capito*, All Periods

SIZE CLASS (mm)	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀	LONG ♂♂	LONG ♀♀	ALL LONG	ALL
0 - 1.0[†]								
1.1- 2.0								
2.1- 3.0	12.50							5.00
3.1- 4.0								
4.1- 5.0		50.00						5.00
5.1- 6.0						25.00	11.11	5.00
6.1- 7.0	12.50				20.00		11.11	10.00
7.1- 8.0	37.50	50.00						20.00
8.1- 9.0								
9.1-10.0	12.50							5.00
10.1-11.0								
11.1-12.0				100.00	20.00		11.11	10.00
12.1-13.0								
13.1-14.0								
14.1-15.0								
15.1-20.0	12.50				40.00	50.00	44.44	25.00
20.1-25.0								
25.1-30.0	12.50						11.11	10.00
30.1-50.0					20.00	25.00	11.11	5.00
>50.0								

[†] Percentage of number of items.

TABLE 5-19. Prey Size - *Anolis biporcatus*, All Periods

SIZE CLASS (mm)	SHORT ♂♂	SHORT ♀♀	MEDIUM ♂♂	MEDIUM ♀♀	LONG ♂♂	LONG ♀♀	ALL LONG	ALL
0 - 1.0[†]		3.23						0.54
1.1- 2.0	9.52	3.23	9.09					3.76
2.1- 3.0		6.45	4.55	3.23	11.11		6.78	4.84
3.1- 4.0	4.76	6.45		3.23	2.78	30.43	13.56	6.45
4.1- 5.0	4.76	19.35	4.55	3.23	8.33	8.70	8.47	8.06
5.1- 6.0	9.52	6.45	6.82	6.45	2.78	4.35	3.39	5.91
6.1- 7.0		6.45	15.91	9.68	8.33		5.08	8.06
7.1- 8.0	33.33	6.45	13.64	9.68	11.11		6.78	11.83
8.1- 9.0	4.76	6.45	4.55	16.13	11.11	13.04	11.86	9.14
9.1-10.0	4.76		2.27	9.68	5.56		3.39	3.76
10.1-11.0	9.52	3.23	11.36	3.23	2.78	8.70	5.08	6.45
11.1-12.0	9.52	3.23	2.27	3.23	2.78		1.69	3.23
12.1-13.0		3.23			8.33		5.08	2.15
13.1-14.0		3.23	2.27	3.23	8.33		5.08	3.23
14.1-15.0	4.76	9.68	15.91	3.23	11.11		6.78	8.60
15.1-20.0	4.76	9.68	4.55	12.90	2.78	4.35	3.39	6.45
20.1-25.0			2.27	3.23		4.35	1.69	1.61
25.1-30.0		3.23		9.68	2.78	13.04	6.78	4.30
30.1-50.0						13.04	5.08	1.61
>50.0								

[†] Percentage of number of items.

TABLE 5-20. Intraspecies (Size) Niche Overlap (L) and Similarity (S) in Prey Taxa

		humilis		*limifrons*		*carpenteri*		*lemurinus*		*lionotus*		*biporcatus*	
CLASSES[†]		S	L	S	L	S	L	S	L	S	L	S	L
LF vs.	LM	0.70	4.84	0.89	2.83	0.53	1.33	0.60	3.50	[Φ]		0.67	2.77
	MF	0.79	5.20	0.78	2.47	0.43	1.56	0.63	8.36	0.34	30.63	0.56	11.79
	MM	0.78	6.64	0.78	2.68	0.65	1.79	0.63	7.54	0.47	2.49	0.66	3.41
	SF	0.72	5.82	0.73	2.57	0.60	4.19	0.64	6.15	0.59	11.63	0.46	2.12
	SM	0.65	6.52	0.72	3.24	0.36	1.04	0.45	3.33	0.56	11.22	0.40	4.05
	UJ	0.67	7.14	0.65	2.19								
LM vs.	MF	0.69	4.78	0.76	2.42	0.50	1.51	0.55	5.73	[Φ]		0.44	4.49
	MM	0.70	5.04	0.75	2.95	0.58	1.44	0.56	4.30	[Φ]		0.68	2.26
	SF	0.66	3.93	0.75	2.96	0.38	0.91	0.52	3.85	[Φ]		0.63	2.19
	SM	0.52	5.67	0.75	3.56	0.50	1.33	0.45	2.39	[Φ]		0.53	2.45
	UJ	0.65	7.66	0.61	2.09								
MF vs.	MM	0.72	5.43	0.74	2.89	0.45	1.45	0.64	7.62	0.16	4.47	0.67	6.02
	SF	0.71	4.67	0.69	2.62	0.56	6.33	0.63	8.22	0.24	34.31	0.38	3.44
	SM	0.69	6.21	0.69	3.24	0.35	1.18	0.46	4.87	0.40	21.47	0.61	8.28
	UJ	0.61	6.61	0.55	2.01								
MM vs.	SF	0.79	6.15	0.74	2.93	0.60	5.49	0.80	10.30	0.42	1.90	0.65	2.25
	SM	0.70	6.63	0.75	3.67	0.63	16.64	0.58	5.53	0.48	3.81	0.64	3.80
	UJ	0.73	8.09	0.64	2.32								
SF vs.	SM	0.71	5.62	0.75	3.80	0.55	17.83	0.59	4.60	0.50	7.85	0.53	2.04
	UJ	0.62	5.92	0.65	2.38								
SM vs.	UJ	0.59	8.41	0.60	2.50								

[†] Abbreviations as in Table 5-3.

[Φ] Sample size of *A. lionotus* long males too small for comparisons.

TABLE 5-21.
Intraspecies (Size) Niche Breadth (B) and Selectivity (G) in Prey Taxa

	humilis		*limifrons*		*carpenteri*	
CLASS[†]	B	G	B	G	B	G
LF	0.12	8.62	0.37	2.74	0.22	4.65
LM	0.17	6.06	0.31	3.18	0.33	3.02
MF	0.16	6.37	0.29	3.45	0.14	7.41
MM	0.12	8.13	0.23	4.27	0.16	6.21
SF	0.18	5.62	0.19	5.21	0.067	14.8
SM	0.13	7.75	0.18	5.49	0.014	69.4
UJ	0.076	13.2	0.28	3.60		
	lemurinus		*lionotus*		*biporcatus*	
LF	0.14	7.19	0.079	12.7	0.15	6.54
LM	0.31	3.23	0.066	15.2	0.34	2.96
MF	0.053	18.8	.0063	159.	0.043	23.4
MM	0.066	15.1	0.34	2.94	0.23	4.39
SF	0.12	8.62	0.067	14.8	0.25	3.95
SM	0.071	14.1	0.041	24.4	0.10	10.0

[†] Abbreviations as in Table 5-3.

TABLE 5-22. Intraspecies (Size) Niche Overlap (L) and Similarity (S) in Prey Length

		humilis		*limifrons*		*carpenteri*		*lemurinus*		*lionotus*		*biporcatus*	
CLASSES[†]		S	L	S	L	S	L	S	L	S	L	S	L
LF vs.	LM	0.78	1.83	0.86	2.06	0.78	1.70	0.68	7.17	Φ		0.33	11.00
	MF	0.80	1.60	0.71	1.30	0.67	1.52	0.52	6.79	0.40	3.93	0.44	36.65
	MM	0.78	1.83	0.84	1.14	0.59	1.17	0.65	3.90	0.73	6.72	0.29	9.05
	SF	0.72	1.03	0.83	1.06	0.52	1.15	0.63	4.00	0.52	9.52	0.37	16.60
	SM	0.86	1.81	0.77	1.18	0.40	0.83	0.53	1.34	0.44	1.66	0.32	7.26
	UJ	0.59	0.89	0.74	1.01								
LM vs.	MF	0.87	1.57	0.75	1.50	0.87	1.64	0.41	2.86	Φ		0.64	27.60
	MM	0.83	1.58	0.86	1.18	0.69	1.10	0.68	4.50	Φ		0.59	39.87
	SF	0.80	1.22	0.86	1.12	0.72	1.27	0.52	2.55	Φ		0.67	33.77
	SM	0.76	1.23	0.81	1.22	0.53	0.85	0.41	0.91	Φ		0.44	19.35
	UJ	0.62	0.78	0.64	0.82								
MF vs.	MM	0.90	1.59	0.82	1.38	0.62	0.86	0.59	6.05	0.38	1.81	0.57	26.58
	SF	0.82	1.23	0.71	1.22	0.80	3.01	0.59	11.34	0.19	1.00	0.61	36.41
	SM	0.82	1.40	0.81	1.38	0.46	0.73	0.48	1.54	0.31	2.92	0.47	21.76
	UJ	0.65	0.97	0.51	0.88								
MM vs.	SF	0.75	1.10	0.86	1.18	0.58	0.68	0.63	3.18	0.58	5.17	0.58	38.00
	SM	0.83	1.31	0.85	1.29	0.58	0.91	0.63	1.32	0.53	1.05	0.62	27.30
	UJ	0.65	0.90	0.67	1.08								
SF vs.	SM	0.77	1.14	0.81	1.21	0.44	0.77	0.41	1.27	0.40	1.14	0.46	20.93
	UJ	0.60	0.83	0.71	0.99								
SM vs.	UJ	0.66	1.01	0.66	1.11								

[†] Abbreviations as in Table 5-3.

[Φ] Sample size of *A. lionotus* long males too small for comparisons.

TABLE 5-23.
Intraspecies (Size) Niche Breadth (B)
and Selectivity (G) in Prey Length

	humilis		*limifrons*		*carpenteri*	
CLASS†	B	G	B	G	B	G
LF	0.43	2.33	0.43	2.33	0.34	2.92
LM	0.34	2.99	0.47	2.15	0.58	1.73
MF	0.61	1.63	0.51	1.95	0.39	2.57
MM	0.44	2.27	0.73	1.37	0.73	1.37
SF	0.80	1.25	0.78	1.28	0.22	4.46
SM	0.45	2.22	0.69	1.45	0.58	1.72
UJ	0.51	1.95	0.66	1.53		

	lemurinus		*lionotus*		*biporcatus*	
	B	G	B	G	B	G
LF	0.097	10.3	0.061	16.4	0.014	69.0
LM	0.11	9.52	0.032	31.3	0.022	45.9
MF	0.039	26.0	0.059	17.0	0.017	57.5
MM	0.22	4.50	0.23	4.39	0.018	56.2
SF	0.15	6.76	0.087	11.5	0.026	38.3
SM	0.56	1.78	0.27	3.76	0.034	29.5

†Abbreviations as in Table 5-3.

TABLE 5-24.
Significance of Intraspecies (Anole Size) Comparisons of Prey Size Distributions

SPECIES	CLASS[†] WITH LONGER MEAN SVL	CLASS WITH SHORTER MEAN SVL	PREY LENGTH BY ITEM SIGNIFICANCE[Φ]	PREY LENGTH BY VOLUME SIGNIFICANCE
humilis	LM	MM	n.s.	***
	LM	SM	n.s.	***
	LM	UJ	***	***
	LF	MF	*	*
	LF	SF	*	***
	LF	UJ	***	***
	LF	LM	n.s.	*
limifrons	LM	MM	n.s.	*
	LM	SM	n.s.	**
	LM	UJ	**	**
	LF	MF	**[∇] (n.s.)[Ψ]	*** (***)
	LF	SF	n.s. (*)	*** (***)
	LF	UJ	* (***)	*** (***)
	LF	LM	n.s. (n.s.)	*** (***)
carpenteri	LM	MM	n.s.	n.s.
	LM	SM	*	*
	LF	MF	n.s.	n.s.
	LF	SF	n.s.	n.s.
	LF	LM	n.s.	n.s.
lemurinus	LM	MM	n.s.	n.s.
	LM	SM	***	**
	LF	MF	n.s.	n.s.
	LF	SF	n.s.	*
	LF	LM	n.s.	***
lionotus	LM	MM	n.s.	**
	LM	SM	*	n.s.
	LF	MF	n.s.	*
	LF	SF	n.s.	*
	LM	LF	n.s.	n.s.
biporcatus	LM	MM	n.s.	*
	LM	SM	n.s.	*
	LF	MF	n.s.	***
	LF	SF	n.s.	***
	LF	LM	n.s.	***

[†] Abbreviations as in Table 5-3.

[Φ] Significance levels as in Table 4-2; Kolmogorov-Smirnov one-tailed test.

[∇] Indicates that the class with smaller lizards had significantly longer prey.

[Ψ] Parentheses are for long females class if 21 small beetles and 19 small spiders are deleted; see text for explanation.

TABLE 5-25.
Regression of Mean Prey Length on Head Length

SPECIES	EQUATION	r	SIGNIFICANCE OF r
humilis	$PL=0.44HL+0.588$	0.932	$P<.01$
limifrons	$PL=0.424HL+0416$	0.943	$P<.01$
carpenteri	$PL=0.629HL-1.81$	0.937	$P<.05$
lemurinus	$PL=0.721HL-2.08$	0.913	$P<.01$
lionotus	$PL=0.469HL+0.512$	0.752	$P<.05$
biporcatus	$PL=1.08HL-10.26$	0.773	$P<.05$

TABLE 5-26.
Prey Size, Number and Volume
Of Large Males and Large Females

			PREY LENGTH		
SPECIES	SEX	PL[†]	SE	N	SIGNIFICANCE[Φ∇]
humilis	♂	4.79	±0.38	77	n.s.
	♀	4.85	±0.26	143	
limifrons	♂	4.32	±0.30	99	n.s.
	♀	4.47	±0.25	205	
carpenteri	♂	3.77	±0.28	27	*
	♀	4.83	±0.43	23	
lemurinus	♂	6.73	±0.66	42	n.s.
	♀	7.74	±0.99	36	
pentaprion	♂	5.90	±0.24	9	**
	♀	4.38	±0.38	16	
lionotus	♂	7.72	±1.89	9	n.s.
	♀	6.56	±0.97	18	
capito	♂	16.64	±3.51	5	n.s.
	♀	20.60	±6.66	4	
biporcatus	♂	11.15	±1.04	36	n.s.
	♀	19.21	±4.30	23	

[†] In millimeters.

[Φ] Significance of difference between males and females; symbols as in Table 4-2.

[∇] t-test.

[Ψ] Mann-Whitney test.

[Θ] In cubic millimeters.

TABLE 5-26 - extended

NUMBER OF ITEMS			PREY VOLUME	
$\overline{NI}$	STOMACHS WITH PREY	SIGNIFICANCE$^{\Psi}$	$\overline{PV}^{\Theta}$	SIGNIFICANCE
2.57	30	*	38.12	*
3.76	38		60.88	
2.48	40	*	25.31	**
4.56	45		57.95	
3.00	9	n.s.	21.08	n.s.
3.83	6		44.21	
3.23	13	n.s.	95.51	***
3.89	9		395.19	
4.50	2	n.s.	68.95	n.s.
5.33	3		59.20	
1.80	5	n.s.	68.14	n.s.
2.57	7		85.71	
2.50	2	n.s.	1020.05	n.s.
1.33	3		532.27	
3.27	11	n.s.	499.45	n.s.
3.29	7		1131.40	

TABLE 5-27.
Seasonal Comparison of Prey Length,
Number and Volume

PREY LENGTH

		PERIOD	$\overline{PL}$	SE	N	SIGNIFICANCE[†][Φ]	
A. humilis	♂♂	SEP	5.49	±0.84	13	SvsN	n.s.
		NOV	4.12	±0.39	32	SvsF	n.s.
		FEB	5.54	±0.97	20	SvsM	n.s.
		MAY	4.59	±1.27	12	NvsF	n.s.
						NvsM	n.s.
						FvsM	n.s.
	♀♀	SEP	6.14	±0.56	34	SvsN	*
		NOV	4.47	±0.51	47	SvsF	n.s.
		FEB	4.70	±0.38	50	SvsM	*
		MAY	3.34	±0.54	12	NvsF	n.s.
						NvsM	n.s.
						FvsM	n.s.
A. limifrons	♂♂	SEP	4.35	±0.51	38	SvsN	n.s.
		NOV	4.76	±0.74	25	SvsF	n.s.
		FEB	3.87	±0.57	15	SvsM	n.s.
		MAY	4.05	±0.47	21	NvsF	n.s.
						NvsM	n.s.
						FvsM	n.s.
	♀♀	SEP	5.63	±0.45	66	SvsN	***
		NOV	3.53	±0.35	18	SvsF	***
		FEB	3.50	±0.25	104	SvsM	n.s.
		MAY	6.78	±1.66	17	NvsF	n.s.
						NvsM	*
						FvsM	***

[†] Significance as in Table 4-2.

[Φ] Kolmogorov-Smirnov test.

[∇] Mann-Whitney test.

[Ψ] Empty stomachs were not included.

TABLE 5-27 - extended

NUMBER OF ITEMS$^{\Psi}$					PREY VOLUME PER STOMACH$^{\Psi}$			
$\overline{NI}$	SE	N STOMACH WITH PREY	SIGNIFICANCE$^{\nabla}$		PV/S	SE	SIGNIFICANCE$^{\nabla}$	
1.86	±0.46	7	SvsN	n.s.	37.57	±12.40	SvsN	n.s.
2.91	±0.56	11	SvsF	n.s.	32.24	±12.25	SvsF	n.s.
3.33	-±0.95	6	SvsM	n.s.	53.20	±16.11	SvsM	n.s.
2.00	±0.52	6	NvsF	n.s.	34.47	±23.81	NvsF	n.s.
			NvsM	n.s.			NvsM	n.s.
			FvsM	n.s.			FvsM	n.s.
3.09	±0.44	11	SvsN	n.s.	76.46	±24.70	SvsN	n.s.
5.22	±0.92	9	SvsF	n.s.	70.61	±21.14	SvsF	n.s.
3.57	±0.68	14	SvsM	n.s.	53.70	±12.96	SvsM	*
3.00	±1.08	4	NvsF	n.s.	21.28	±13.18	NvsF	n.s.
			NvsM	n.s.			NvsM	*
			FvsM	n.s.			FvsM	n.s.
2.71	±0.46	14	SvsN	n.s.	33.17	± 6.64	SvsN	n.s.
2.50	±0.56	10	SvsF	n.s.	18.53	± 3.82	SvsF	n.s.
2.14	±0.83	7	SvsM	n.s.	29.36	±17.90	SvsM	n.s.
2.33	±0.44	9	NvsF	n.s.	17.46	± 5.71	NvsF	n.s.
			NvsM	n.s.			NvsM	n.s.
			FvsM	n.s.			FvsM	n.s.
3.47	±0.43	19	SvsN	n.s.	70.77	±18.46	SvsN	n.s.
4.50	±2.22	4	SvsF	n.s.	25.43	± 6.50	SvsF	n.s.
7.43	±2.55	14	SvsM	*	48.79	± 7.72	SvsM	n.s.
2.13	±0.30	8	NvsF	n.s.	59.80	±22.65	NvsF	n.s.
			NvsM	n.s.			NvsM	n.s.
			FvsM	n.s.			FvsM	n.s.

TABLE 5-28.
Number of Empty Stomachs in May Compared
With Other Collection Periods

		x^2	significance[Φ]
A. humilis	♂♂[†]		
	SEP	4.55	*
	NOV	14.26	***
	FEB	5.21	*
	♀♀		
	SEP	8.96	**
	NOV	12.12	***
	FEB	11.89	***
A. limifrons	♂♂		
	SEP	34.94	***
	NOV	28.24	***
	FEB	10.61	**
	♀♀		
	SEP	23.94	***
	NOV	15.01	***
	FEB	13.63	***

[†] Includes all males or females of each period not just large.

[Φ] Significance as in Table 4-2: in all cases May has a greater proportion empty; 2 x 2 chi-squared test.

TABLE 5-29.
Overlap and Similarity by Period

		PREY LENGTH		PREY TAXA	
A. humilis ♂♂		S	L	S	L
SEP vs.	NOV	0.52	1.02	0.48	3.31
	FEB	0.41	2.97	0.58	9.35
	MAY	0.47	1.19	0.56	3.75
NOV vs.	FEB	0.39	1.08	0.40	4.05
	MAY	0.44	0.49	0.64	3.78
FEB vs.	MAY	0.55	7.73	0.48	5.39
♀♀					
SEP vs.	NOV	0.64	2.39	0.46	3.78
	FEB	0.66	2.63	0.50	4.27
	MAY	0.41	0.88	0.34	5.32
NOV vs.	FEB	0.80	1.73	0.74	11.38
	MAY	0.61	1.00	0.46	2.88
FEB vs.	MAY	0.56	0.93	0.52	2.09
A. limifrons ♂♂					
SEP vs.	NOV	0.72	2.75	0.73	2.27
	FEB	0.71	1.24	0.68	3.19
	MAY	0.79	1.38	0.64	2.96
NOV vs.	FEB	0.63	0.90	0.65	3.06
	MAY	0.69	1.11	0.61	3.26
FEB vs.	MAY	0.74	0.92	0.47	2.44
♀♀					
SEP vs.	NOV	0.48	0.90	0.55	1.52
	FEB	0.47	1.80	0.63	2.41
	MAY	0.63	4.74	0.72	3.95
NOV vs.	FEB	0.66	1.00	0.62	1.96
	MAY	0.45	0.83	0.45	1.52
FEB vs.	MAY	0.47	2.67	0.66	3.08

TABLE 5-30.
Significance of Difference In Prey Size of Large Size Classes

	FEMALES							
MALES	*humilis*	*limifrons*	*carpenteri*	*lemurinus*	*pentaprion*	*lionotus*	*capito*	*biporcatus*
humilis		(*)[Φ][∇]	n.s.	*	n.s.	n.s.	*	***
limifrons	n.s.[†]		**[∇]	***	n.s.	*[∇]	**	***
carpenteri	n.s.	n.s.		n.s.	n.s.	n.s.	*	**
lemurinus	***	***	**		*	n.s.	*	*
pentaprion	**	***	**	n.s.		n.s.	*	**
lionotus	n.s.	n.s.	n.s.	n.s.	n.s.		*	n.s.
capito	**	**	**	**	*	n.s.		n.s.
biporcatus	***	***	***	***	***	n.s.	n.s.	

[†] Significance as in Table 4-2.

[Φ] Parentheses indicate that the shorter predator had significantly more long prey.

[∇] If 19 small spiders from a single female *A. limifrons* and 21 small beetles from another female *A. limifrons* are deleted, these differences are not significant.

TABLE 5-31.
Interspecies Similarity in Prey Length and Taxa

TAXA

LENGTH	*humilis*	*limifrons*	*carpenteri*	*lemurinus*	*pentaprion*	*lionotus*	*capito*	*biporcatus*
humilis		0.64	0.65	0.63	0.29	0.69	0.39	0.48
limifrons	0.85		0.80	0.61	0.35	0.52	0.36	0.50
carpenteri	0.74	0.67		0.60	0.44	0.56	0.34	0.54
lemurinus	0.67	0.56	0.56		0.41	0.52	0.48	0.80
pentaprion	0.53	0.47	0.62	0.50		0.37	0.11	0.43
lionotus	0.74	0.63	0.60	0.65	0.53		0.45	0.48
capito	0.15	0.12	0.16	0.27	0.19	0.26		0.45
biporcatus	0.51	0.40	0.40	0.57	0.36	0.60	0.32	

TABLE 5-32.
Interspecies Overlap in Prey Length and Taxa

TAXA

LENGTH	*humilis*	*limifrons*	*carpenteri*	*lemurinus*	*pentaprion*	*lionotus*	*capito*	*biporcatus*
humilis		3.09	2.19	4.11	1.00	7.27	7.99	2.59
limifrons	1.70		2.02	2.78	1.38	3.96	5.48	2.16
carpenteri	1.35	1.22		1.62	1.73	1.76	1.21	1.15
lemurinus	3.16	2.17	1.23		1.28	5.50	8.39	3.19
pentaprion	1.23	1.03	1.54	1.41		1.13	0.41	1.40
lionotus	3.45	2.00	1.12	5.63	1.16		14.70	4.31
capito	11.10	8.48	0.32	32.69	0.74	31.60		7.86
biporcatus	4.36	4.39	1.36	9.35	1.10	11.37	67.95	

TABLE 5-33.
Niche Breadth and Selectivity
In Prey Length and Taxa

	LENGTH		TAXA	
SPECIES	B	G	B	G
humilis	0.46	2.17	0.15	6.58
limifrons	0.46	2.17	0.35	2.82
carpenteri	0.51	1.96	0.40	2.52
lemurinus	0.12	8.33	0.24	4.18
pentaprion	0.33	3.03	0.26	3.91
lionotus	0.073	13.70	0.089	11.29
capito	0.0027	370.37	0.035	28.41
biporcatus	0.031	32.36	0.29	3.41

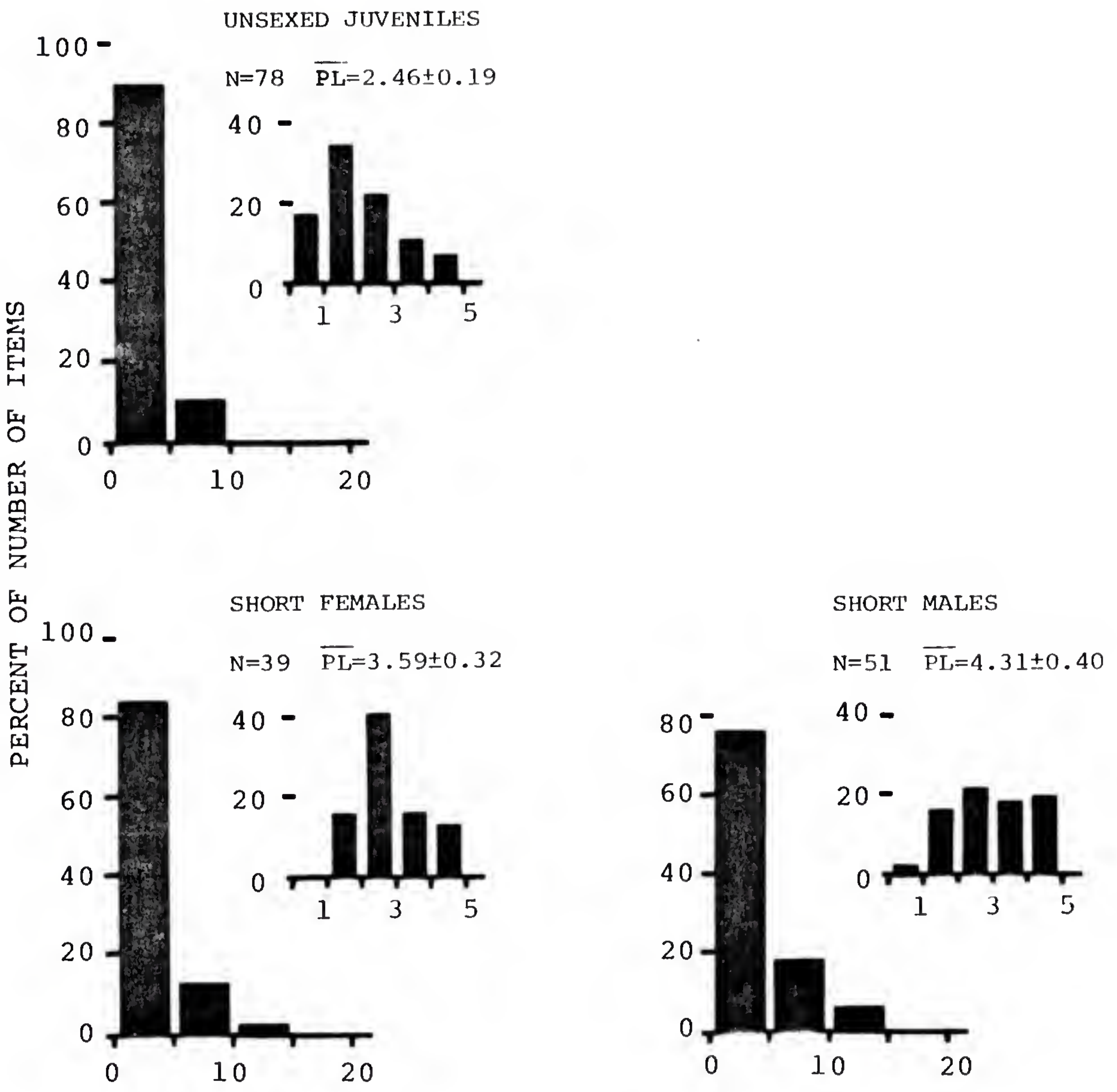
TABLE 5-34
Comparison of Prey Size Distributions In Similar Sized interspecies Pairs

SMALLER SPECIES	LARGER SPECIES	SIGNIFICANCE[†]
Different Habitats		
M[Φ] *humilis*	S *limifrons*	n.s.
M *humilis*	S *carpenteri*	n.s.
M *humilis*	S *lemurinus*	n.s.
S *limifrons*	S *carpenteri*	n.s.
S *carpenteri*	S *lemurinus*	n.s.
L *humilis*	M *limifrons*	n.s.
L *humilis*	M *carpenteri*	n.s.
L *humilis*	S *lionotus*	(***)[∇]
M *limifrons*	S *lionotus*	(***)
M *limifrons*	M *carpenteri*	n.s.
M *carpenteri*	S *lionotus*	(**)
L *limifrons*	S *pentaprion*	n.s.
L *carpenteri*	M *lemurinus*	**
M *lemurinus*	S *pentaprion*	n.s.
M *lemurinus*	S *capito*	n.s.
S *pentaprion*	S *capito*	**
L *lemurinus*	M *pentaprion*	(*)
L *lemurinus*	M *lionotus*	n.s.
M *pentaprion*	M *lionotus*	n.s.
M *lionotus*	S *capito*	*
L *lionotus*	S *biporcatus*	*
L *capito*	M *biporcatus*	n.s.
Same Habitat		
S *limifrons*	S *lemurinus*	n.s.
L *limifrons*	L *lemurinus*	***
L *carpenteri*	L *pentaprion*	n.s.
L *humilis*	L *capito*	**
L *limifrons*	L *biporcatus*	***
L *lemurinus*	L *biporcatus*	**

[†] Significance as in Table 4-2; Kolmogorov-Smirnov one-tailed test.

[Φ] S, short, both mexes; M, medium, both sexes; L, long, both sexes.

[∇] Parentheses indicate that the smaller species had significantly more large prey items.


PERCENT OF NUMBER OF ITEMS
UNSEXED JUVENILES
N=78 $\overline{PL}$=2.46±0.19
100
80
60
40
20
0
0
10
20
40
20
0
1
3
5
SHORT FEMALES
N=39 $\overline{PL}$=3.59±0.32
100
80
60
40
20
0
0
10
20
40
20
0
1
3
5
SHORT MALES
N=51 $\overline{PL}$=4.31±0.40
80
60
40
20
0
0
10
20
40
20
0
1
3
5

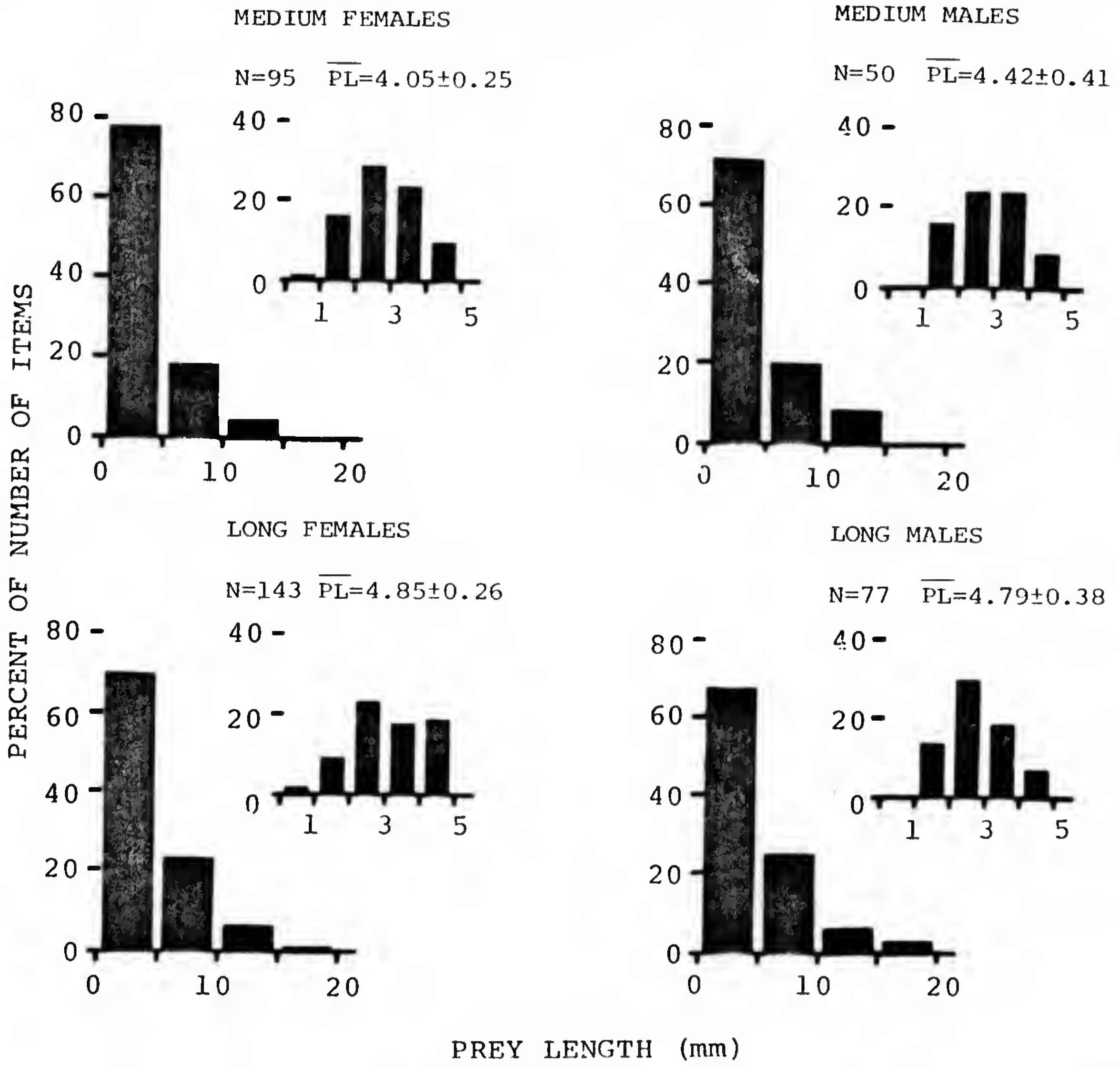
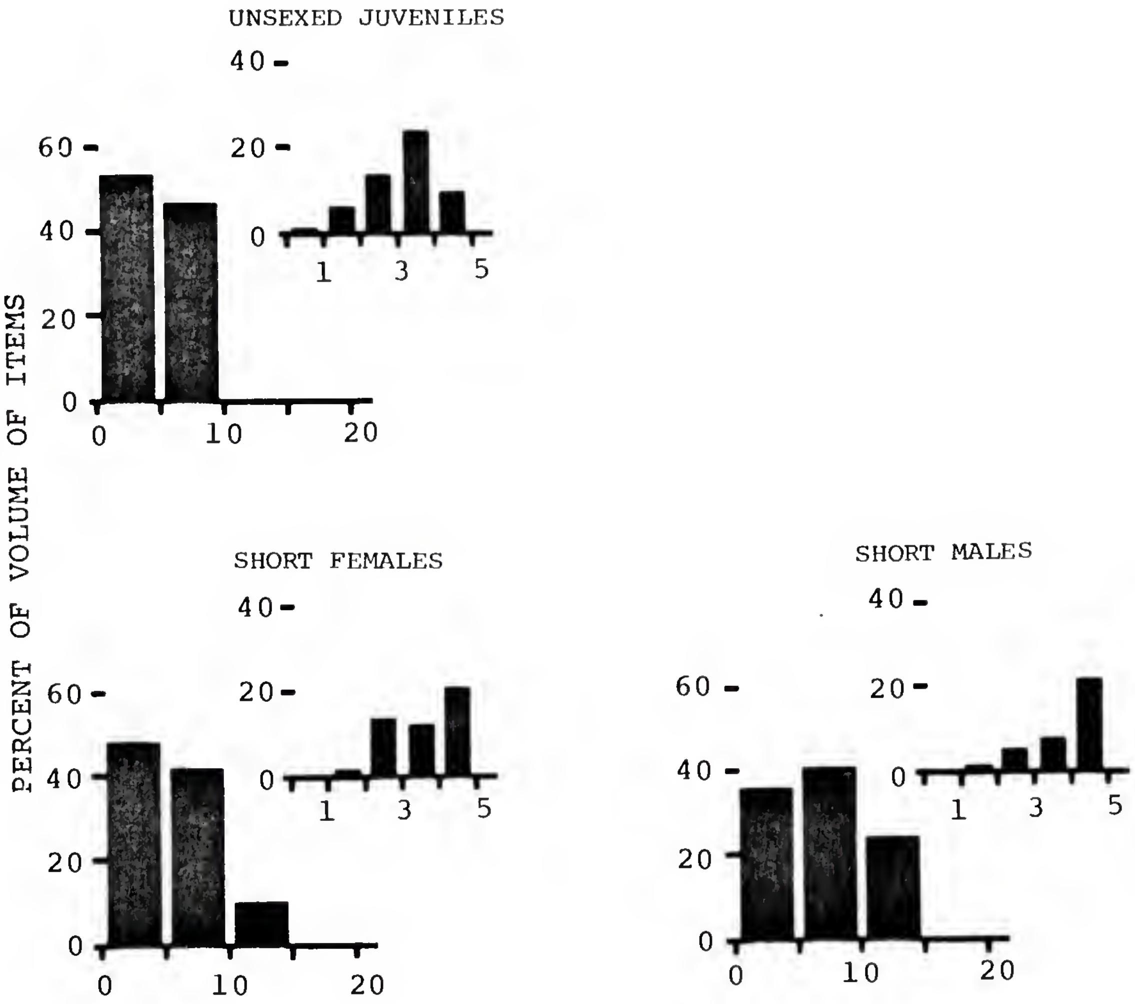


FIGURE 5-1. Distribution of Prey by Frequency According to Prey Length for *Anolis humilis*.


UNSEXED JUVENILES
SHORT FEMALES
SHORT MALES
PERCENT OF VOLUME OF ITEMS
0
20
40
60
0
10
20
1
3
5

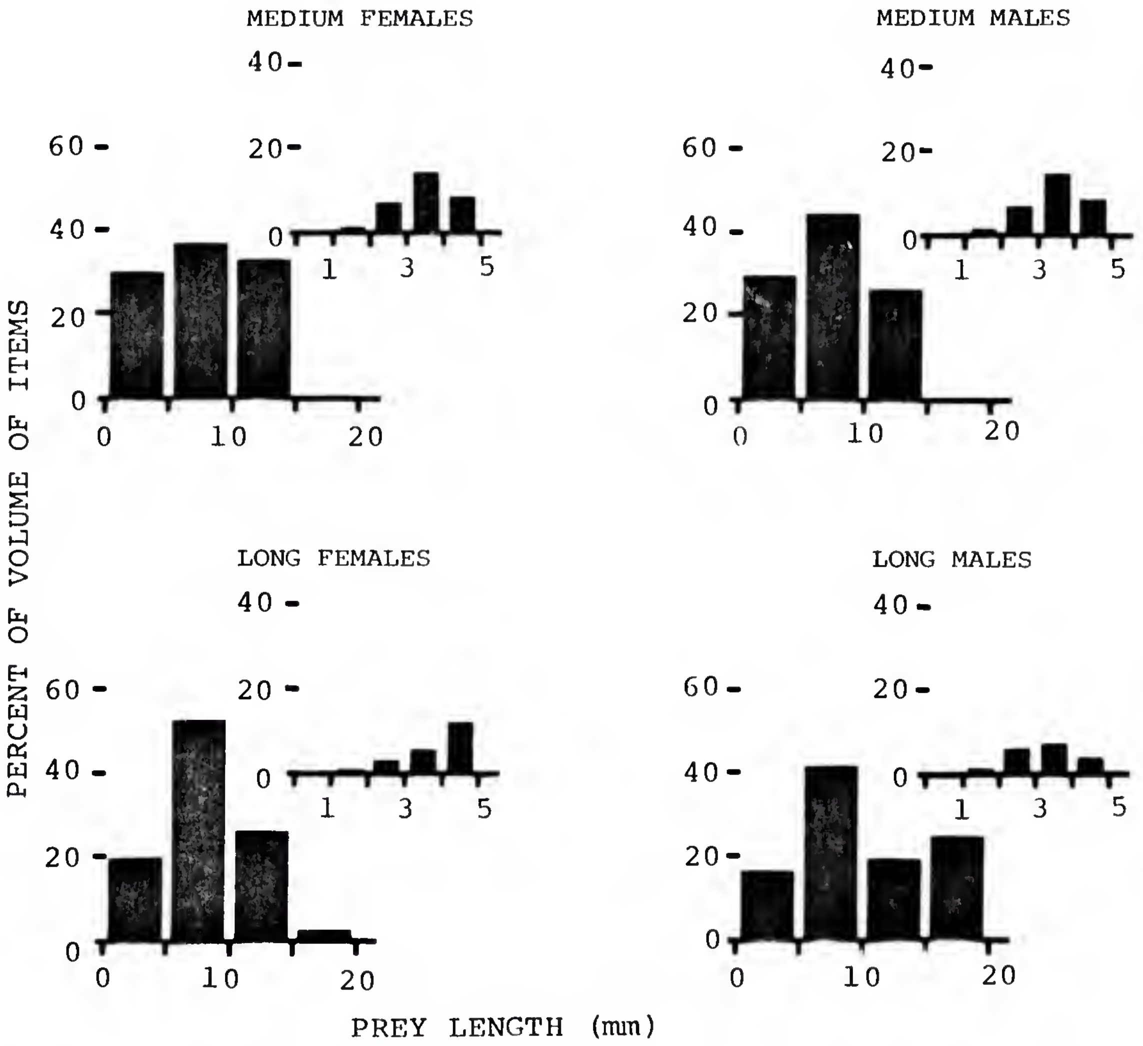
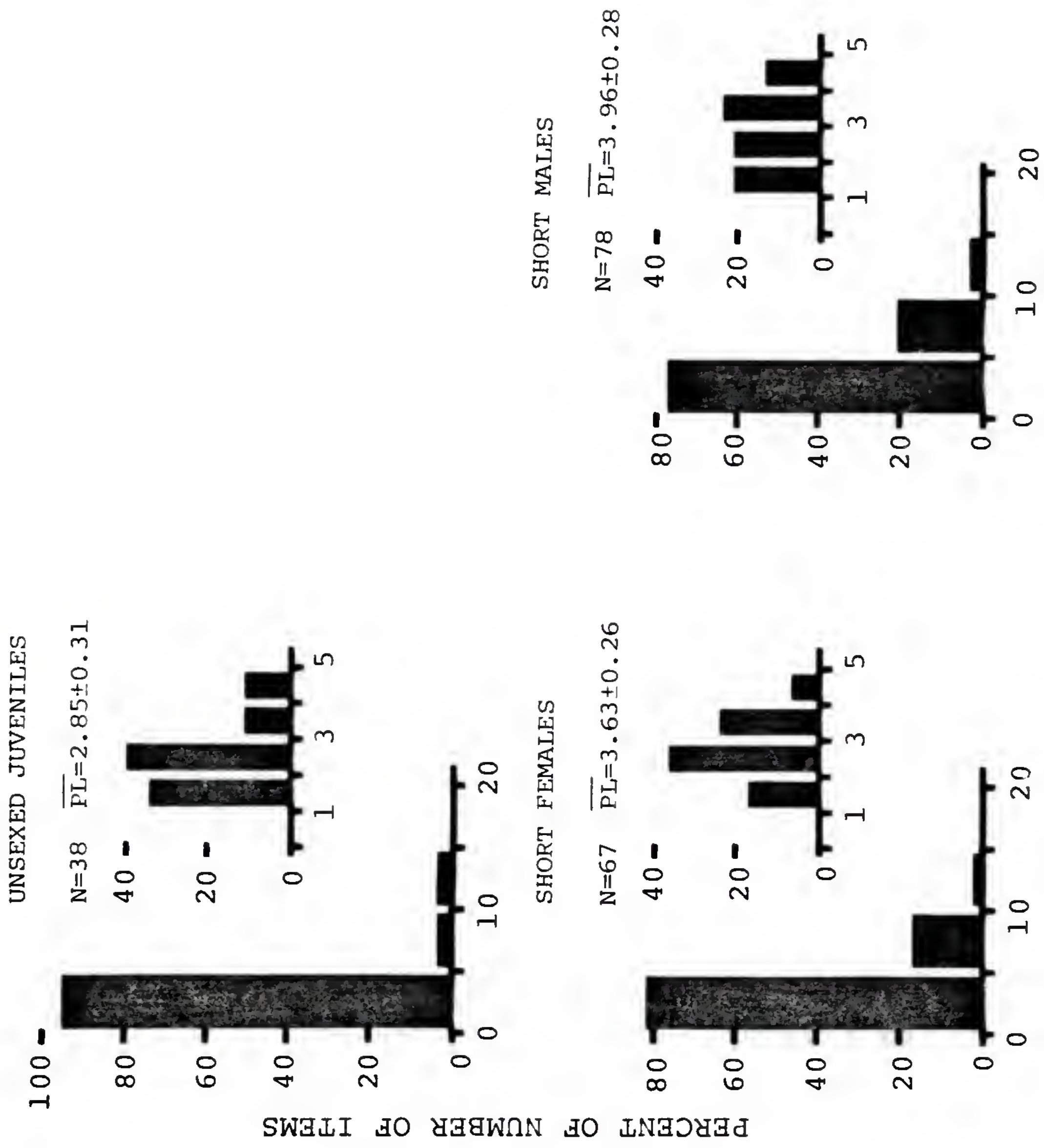


FIGURE 5-2. Distribution of Prey by Volume According to Prey Length for *Anolis humilis*.


PERCENT OF NUMBER OF ITEMS
UNSEXED JUVENILES
N=38 $\overline{PL}$=2.85±0.31
SHORT FEMALES
N=67 $\overline{PL}$=3.63±0.26
SHORT MALES
N=78 $\overline{PL}$=3.96±0.28
100
80
60
40
20
0
10
20
1
3
5

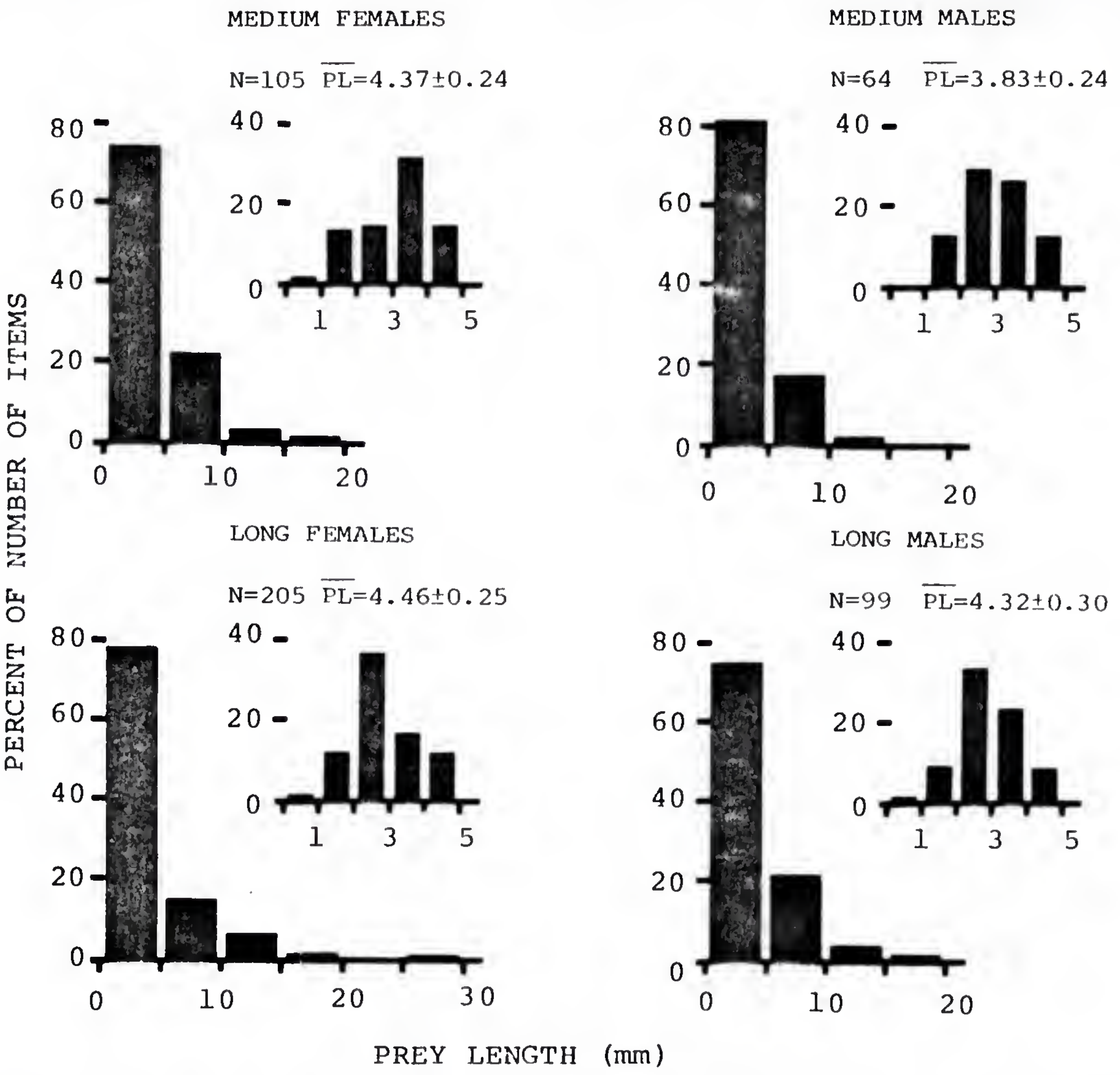
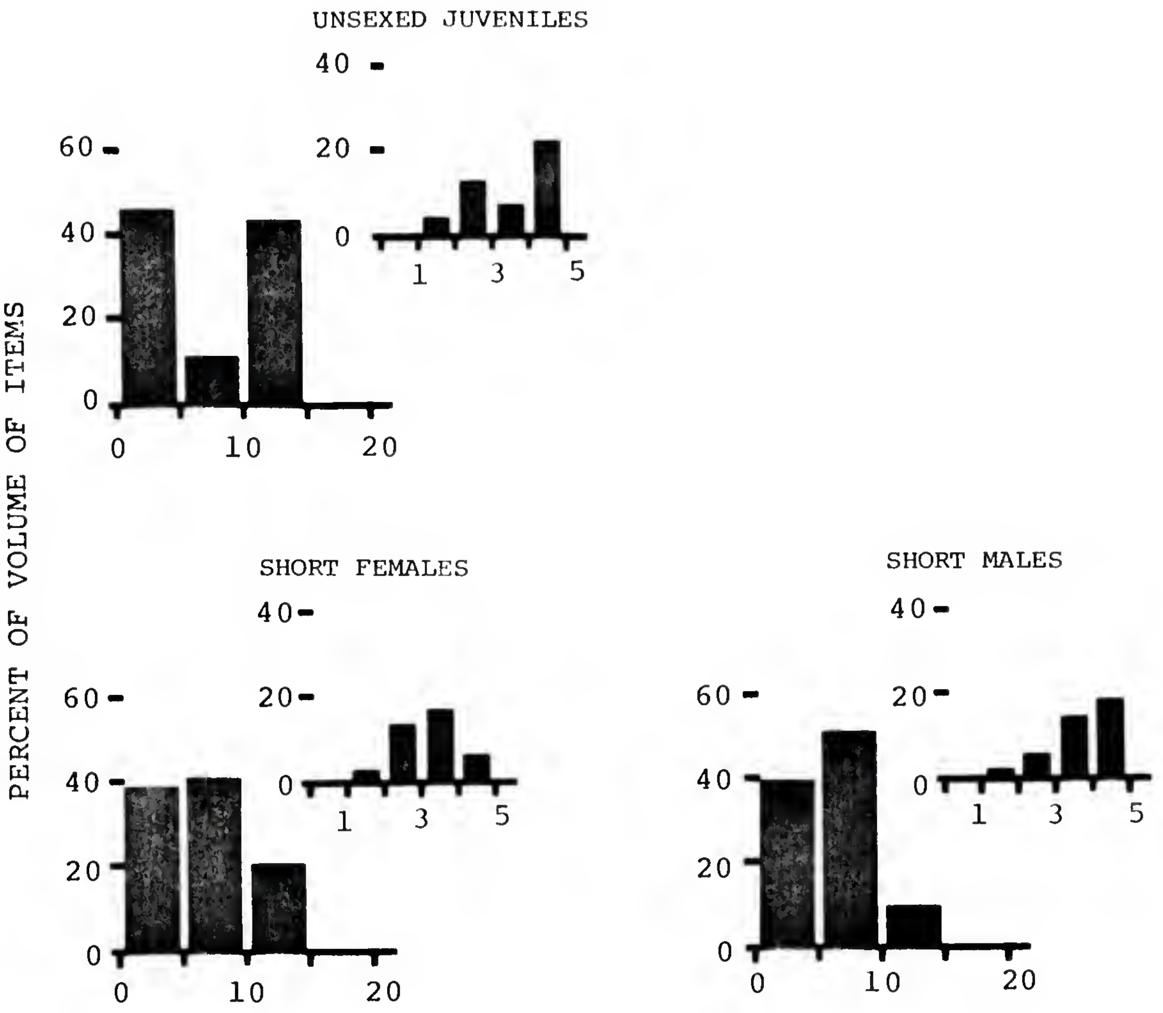


FIGURE 5-3. Distribution of Prey by Frequency According to Prey Length for *Anolis limifrons*.


UNSEXED JUVENILES
SHORT FEMALES
SHORT MALES
PERCENT OF VOLUME OF ITEMS
60
40
20
0
0
10
20
40
20
0
1
3
5

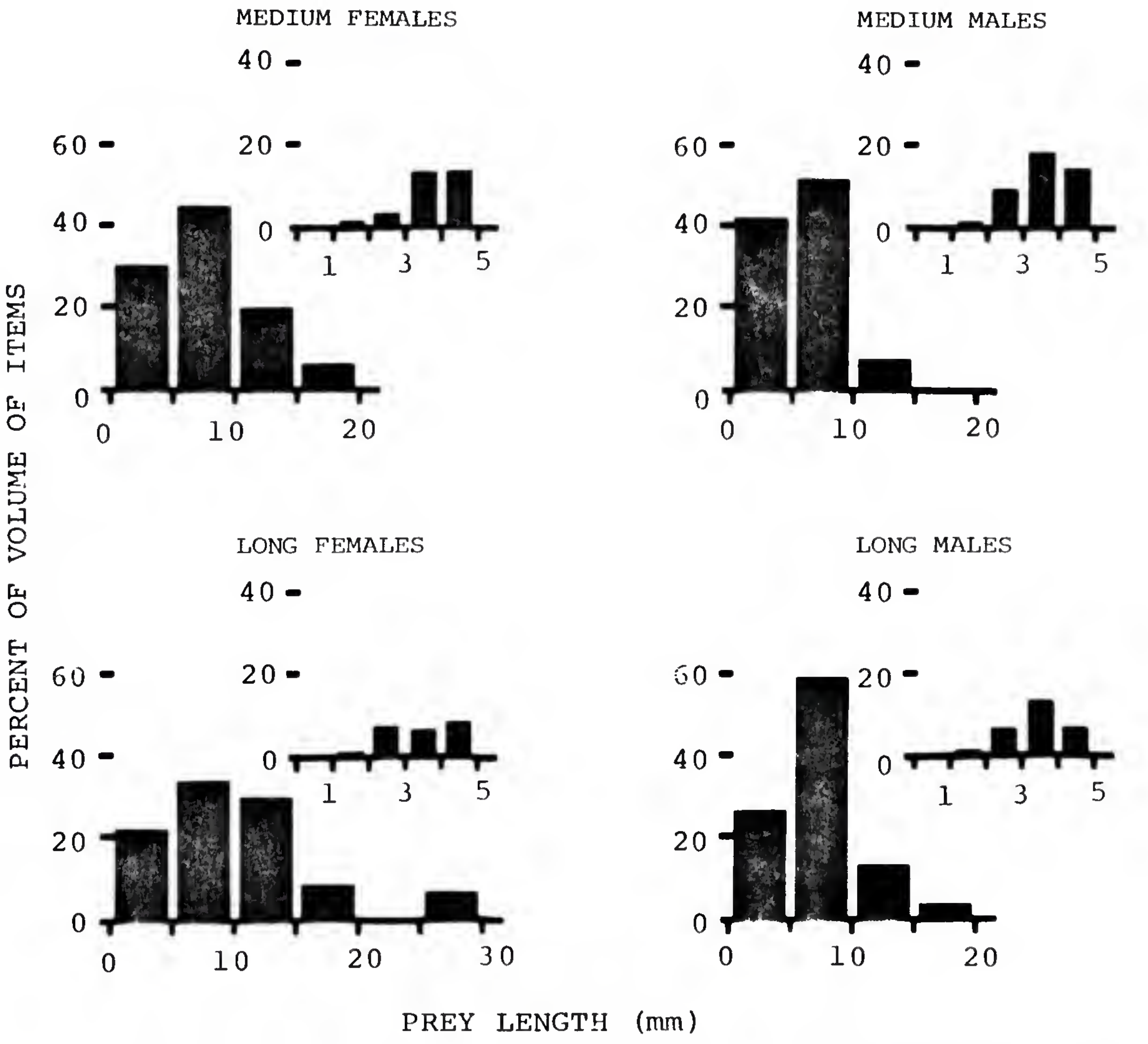


FIGURE 5-4. Distribution of Prey by Volume According to Prey Length for *Anolis limifrons*.

FIGURE 5-5. Distribuiton of Prey by Frequency According to Prey Length for *Anolis carpenteri*.

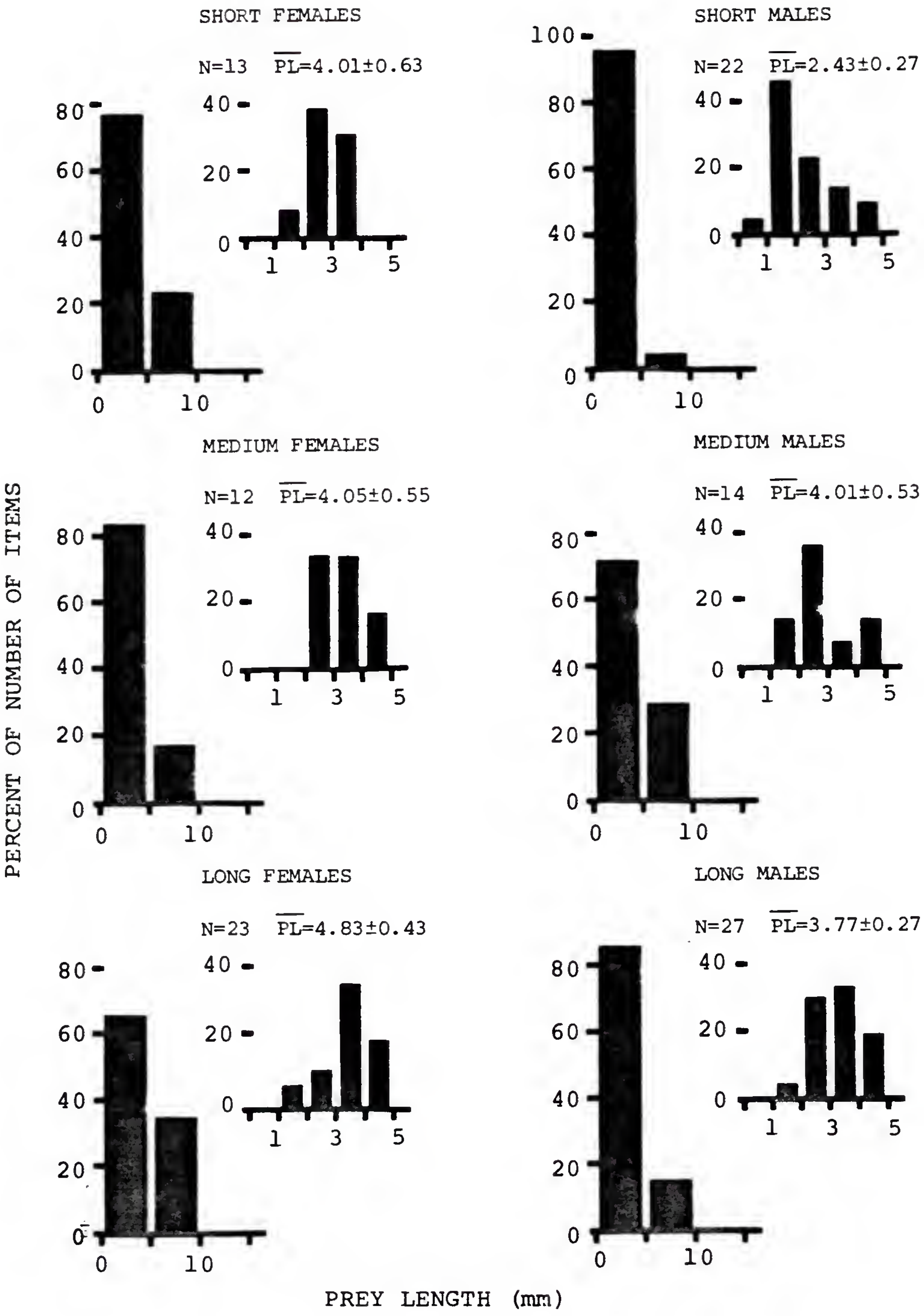

SHORT FEMALES
N=13 PL=4.01±0.63
SHORT MALES
N=22 PL=2.43±0.27
MEDIUM FEMALES
N=12 PL=4.05±0.55
MEDIUM MALES
N=14 PL=4.01±0.53
LONG FEMALES
N=23 PL=4.83±0.43
LONG MALES
N=27 PL=3.77±0.27
100
80
60
40
20
0
10
1
3
5
PERCENT OF NUMBER OF ITEMS
PREY LENGTH (mm)

FIGURE 5-6. Distribution of Prey by Volume According to Prey Length for *Anolis carpenteri*.

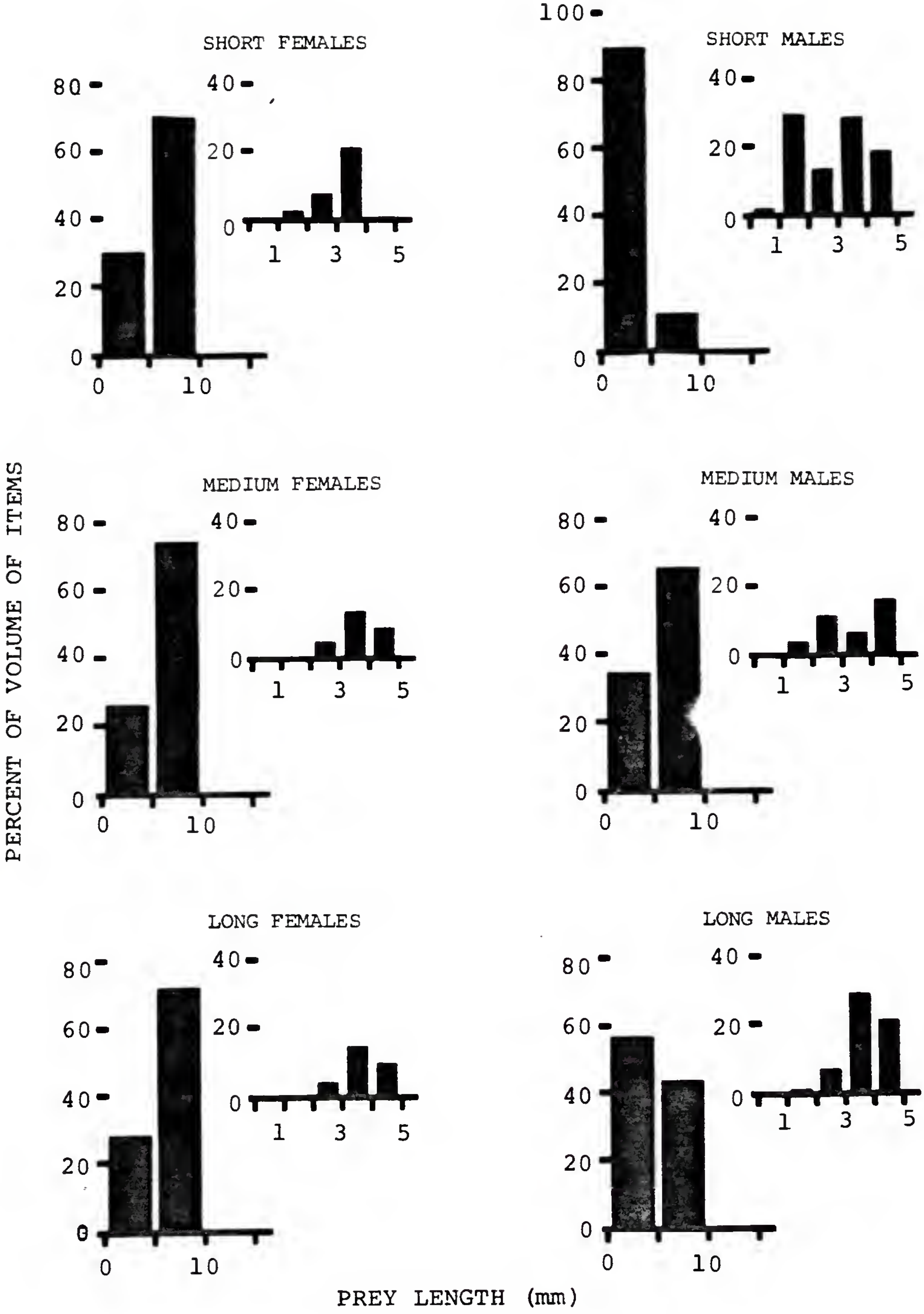

SHORT FEMALES
80
60
40
20
0
0
10
40
20
0
1
3
5
SHORT MALES
100
80
60
40
20
0
0
10
40
20
0
1
3
5
MEDIUM FEMALES
80
60
40
20
0
0
10
40
20
0
1
3
5
MEDIUM MALES
80
60
40
20
0
0
10
40
20
0
1
3
5
LONG FEMALES
80
60
40
20
0
0
10
40
20
0
1
3
5
LONG MALES
80
60
40
20
0
0
10
40
20
0
1
3
5
PERCENT OF VOLUME OF ITEMS
PREY LENGTH (mm)

FIGURE 5-7. Distribution of Prey by Frequency According to Prey Length for *Anolis lemurinus*.

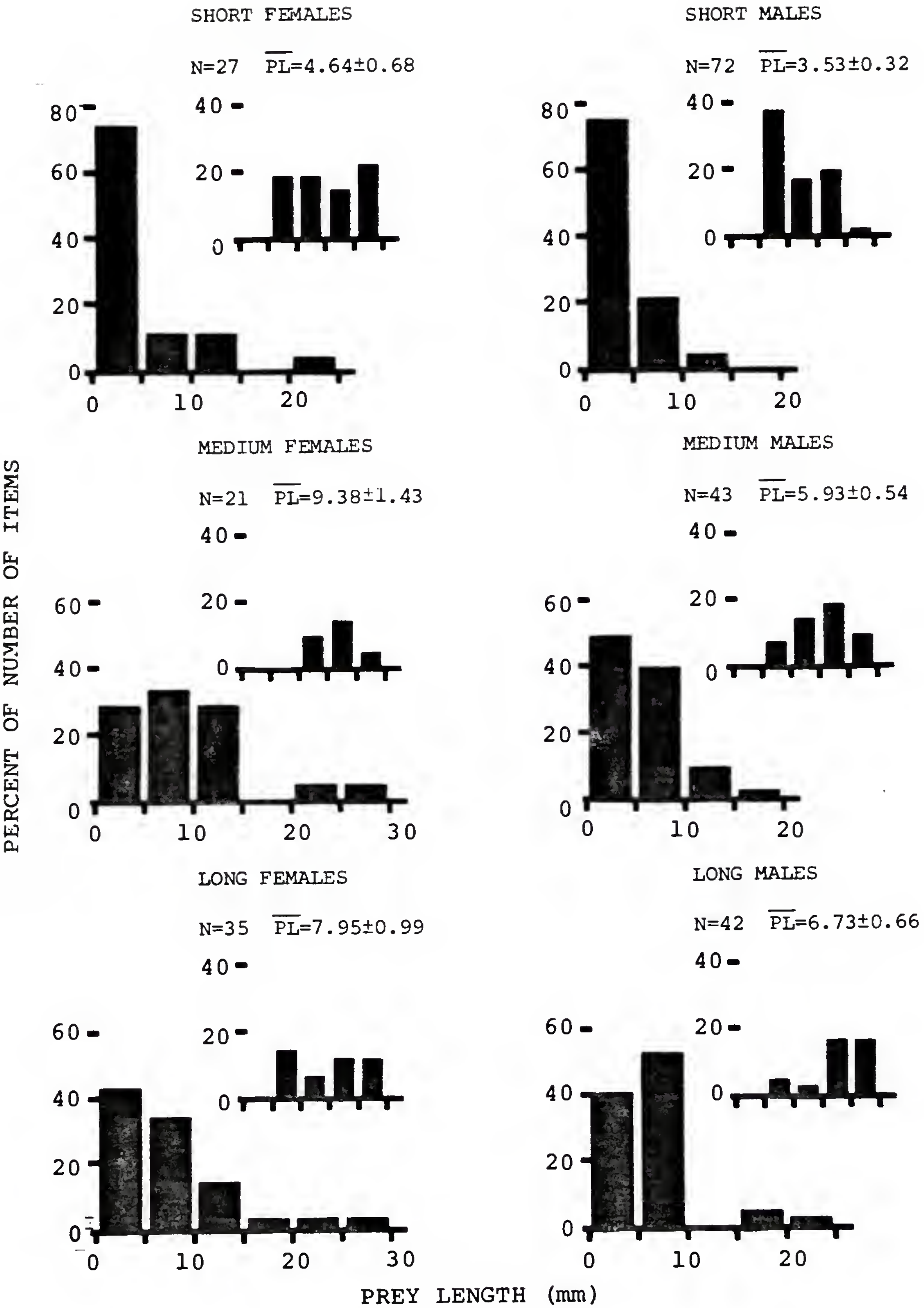

SHORT FEMALES
N=27 $\overline{PL}$=4.64±0.68
SHORT MALES
N=72 $\overline{PL}$=3.53±0.32
MEDIUM FEMALES
N=21 $\overline{PL}$=9.38±1.43
MEDIUM MALES
N=43 $\overline{PL}$=5.93±0.54
LONG FEMALES
N=35 $\overline{PL}$=7.95±0.99
LONG MALES
N=42 $\overline{PL}$=6.73±0.66
80
60
40
20
0
10
30
PERCENT OF NUMBER OF ITEMS
PREY LENGTH (mm)

FIGURE 5-8. Distribution of Prey by Volume According to Prey Length for *Anolis lemurinus*.

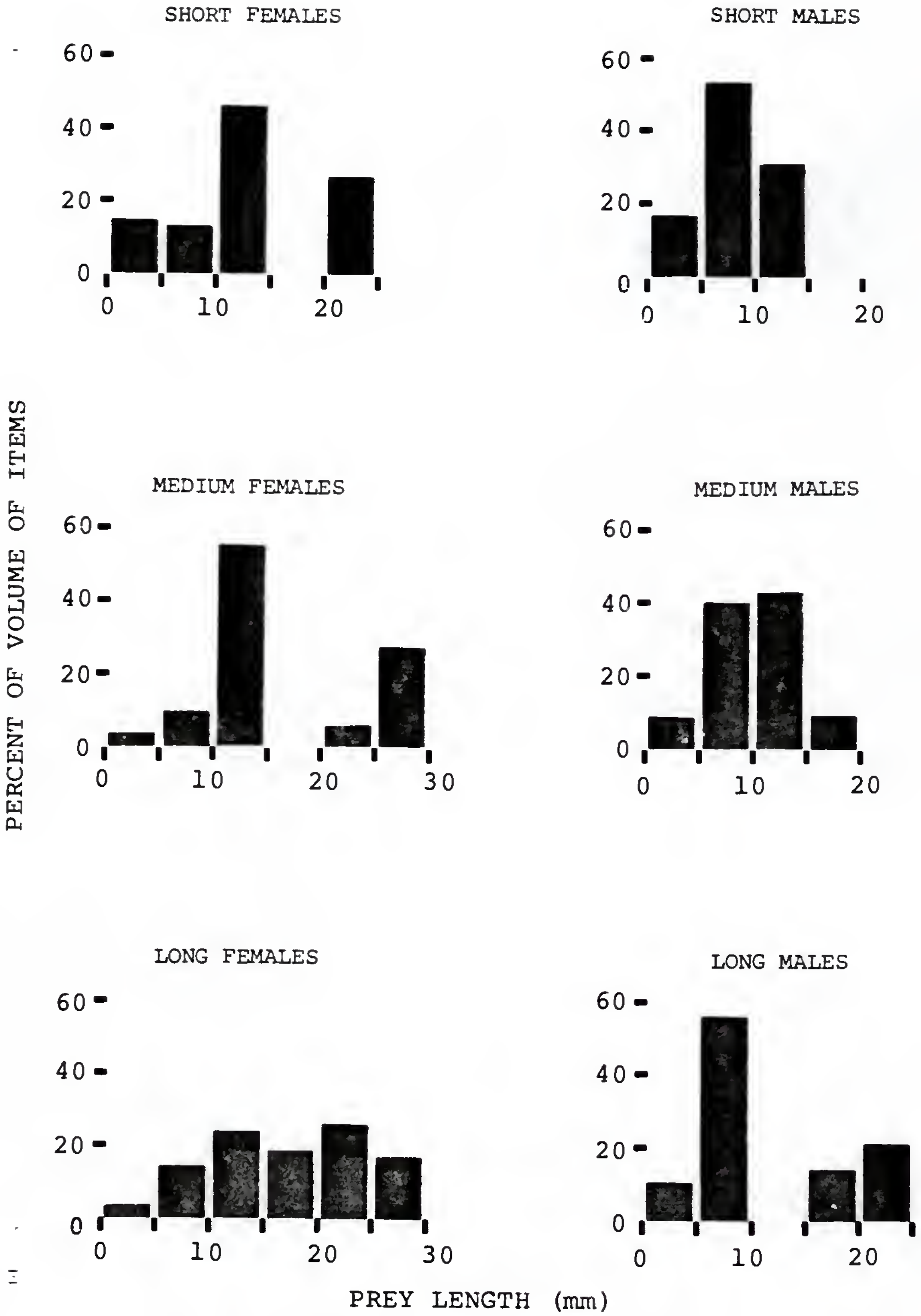
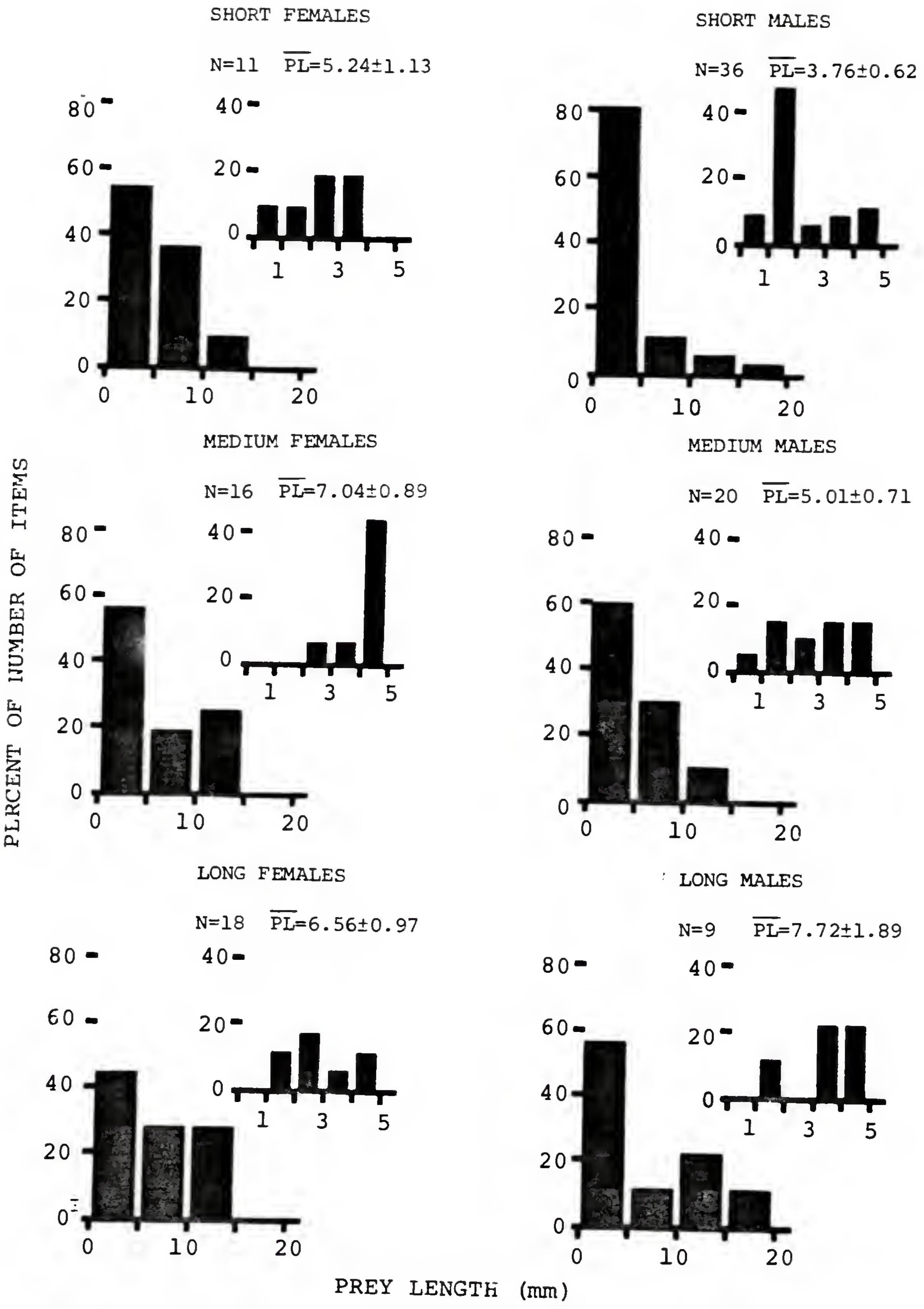

SHORT FEMALES
SHORT MALES
MEDIUM FEMALES
MEDIUM MALES
LONG FEMALES
LONG MALES
60
40
20
0
0
10
20
30
PERCENT OF VOLUME OF ITEMS
PREY LENGTH (mm)

FIGURE 5-9. Distribution of Prey by Frequency According to Prey Length for *Anolis lionotus*.



SHORT FEMALES

N=11 $\overline{PL}$=5.24±1.13

SHORT MALES

N=36 $\overline{PL}$=3.76±0.62

MEDIUM FEMALES

N=16 $\overline{PL}$=7.04±0.89

MEDIUM MALES

N=20 $\overline{PL}$=5.01±0.71

LONG FEMALES

N=18 $\overline{PL}$=6.56±0.97

LONG MALES

N=9 $\overline{PL}$=7.72±1.89

FIGURE 5-10. Distribution of Prey by Volume According to Prey Length for *Anolis lionotus*.

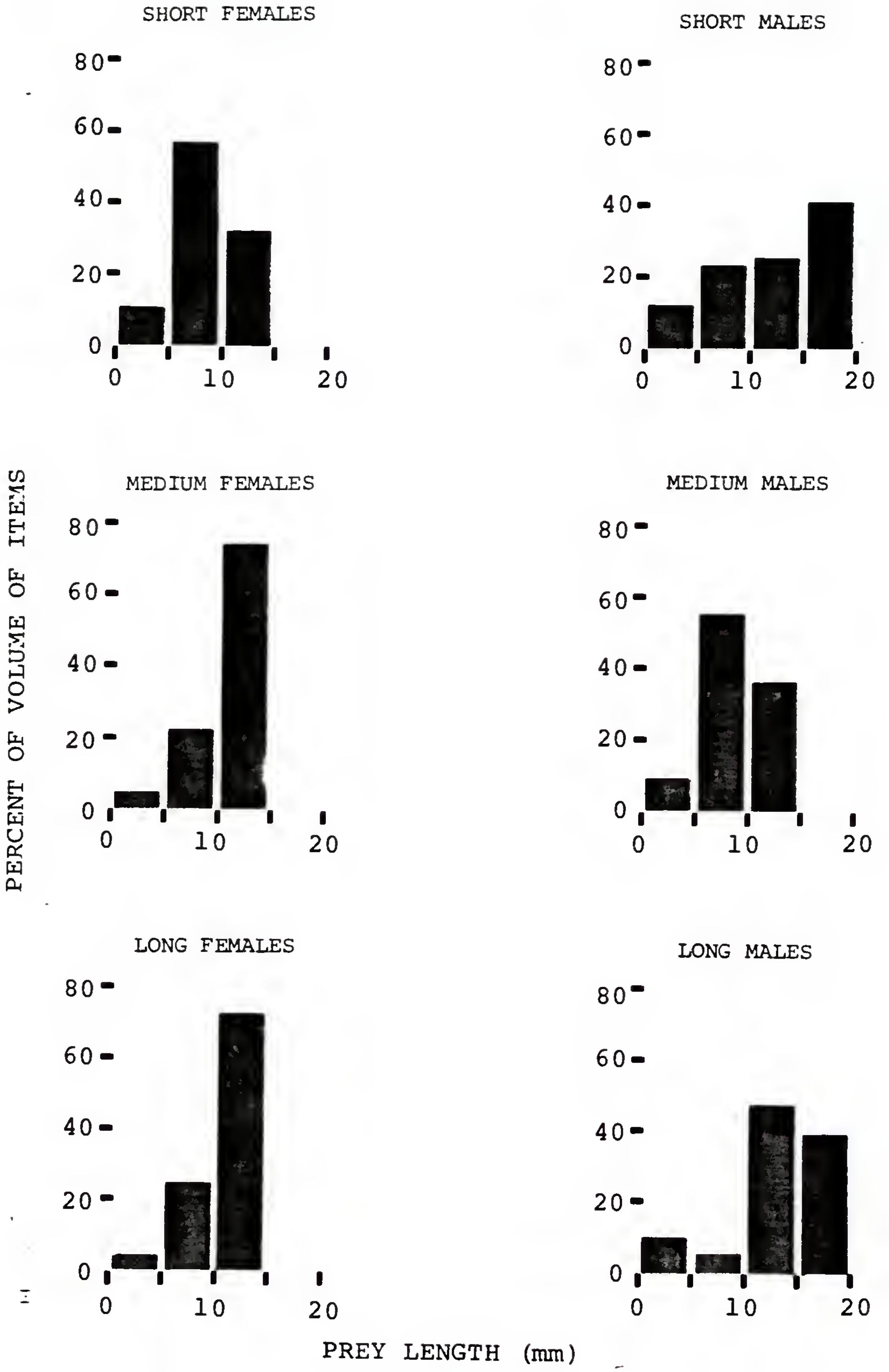

SHORT FEMALES
SHORT MALES
MEDIUM FEMALES
MEDIUM MALES
LONG FEMALES
LONG MALES
PERCENT OF VOLUME OF ITEMS
PREY LENGTH (mm)
0
20
40
60
80
0
10
20

FIGURE 5-11. Distribution of Prey by Frequency According to Prey Length for *Anolis biporcatus*.

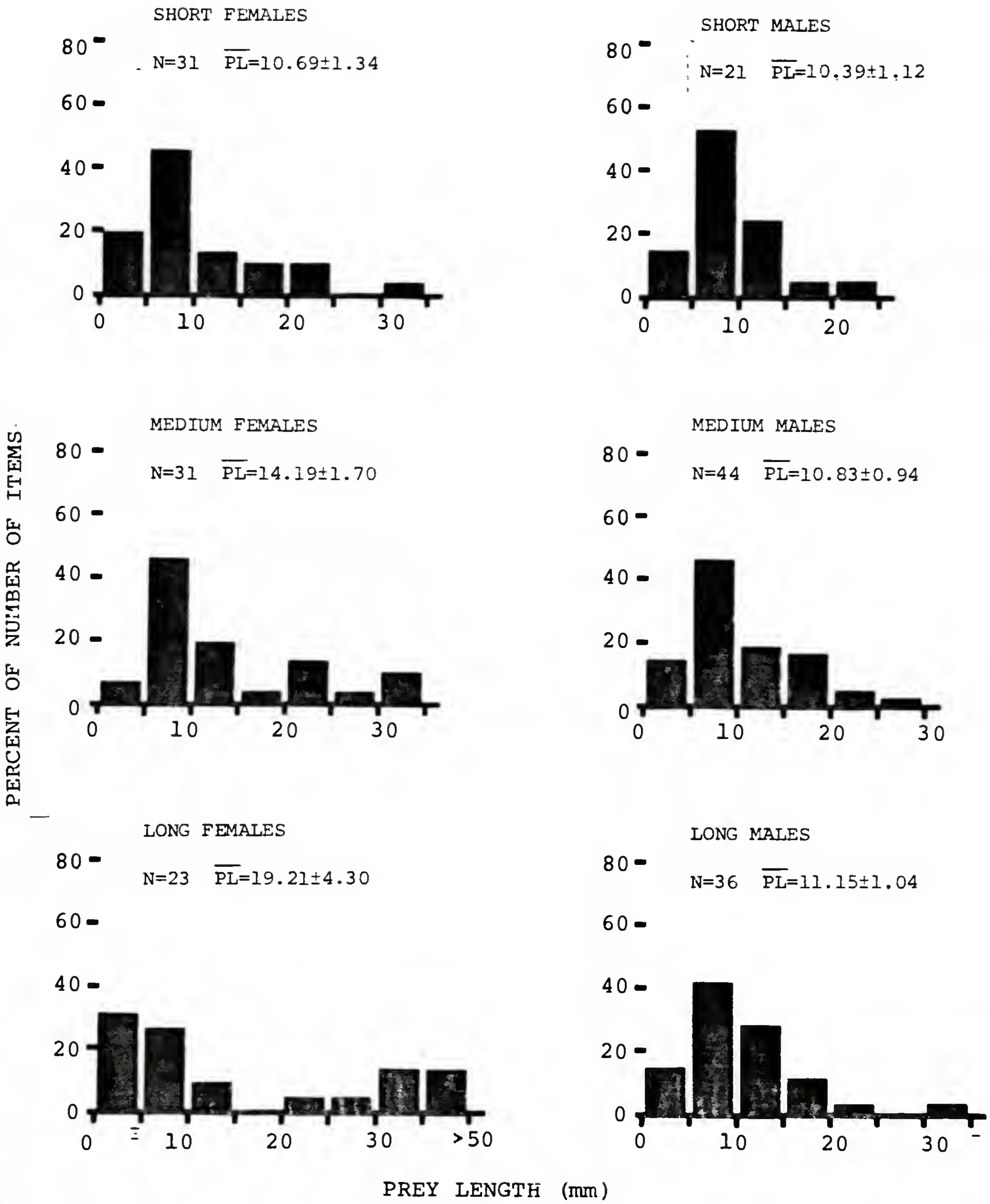

SHORT FEMALES
N=31 $\overline{PL}$=10.69±1.34
SHORT MALES
N=21 $\overline{PL}$=10.39±1.12
MEDIUM FEMALES
N=31 $\overline{PL}$=14.19±1.70
MEDIUM MALES
N=44 $\overline{PL}$=10.83±0.94
LONG FEMALES
N=23 $\overline{PL}$=19.21±4.30
LONG MALES
N=36 $\overline{PL}$=11.15±1.04
0
20
40
60
80
0
10
20
30
>50
PERCENT OF NUMBER OF ITEMS
PREY LENGTH (mm)

FIGURE 5-12. Distribution of Prey by Volume According to Prey Length for *Anolis biporcatus*.

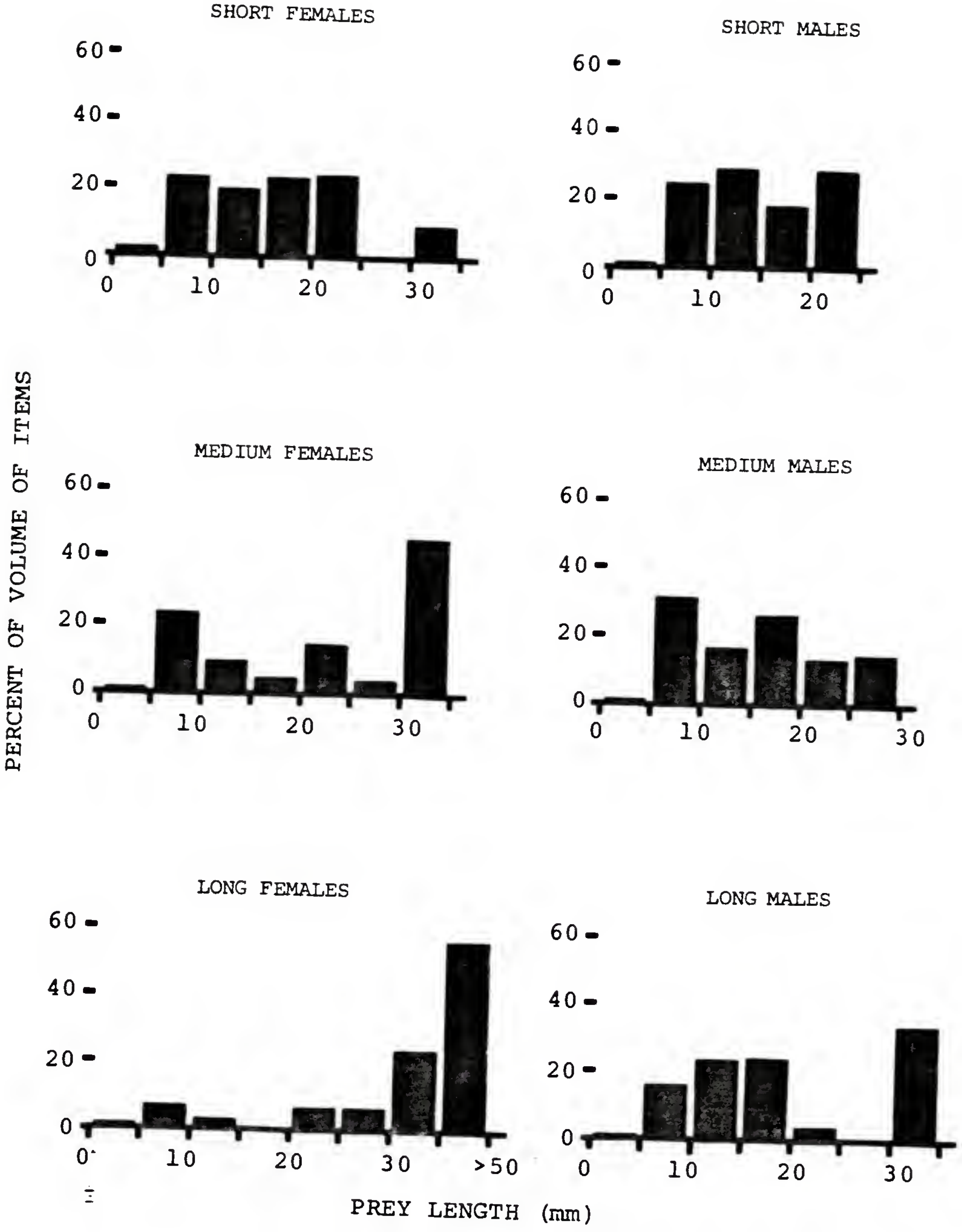

SHORT FEMALES
SHORT MALES
MEDIUM FEMALES
MEDIUM MALES
LONG FEMALES
LONG MALES
PERCENT OF VOLUME OF ITEMS
PREY LENGTH (mm)
0
20
40
60
0
10
20
30
>50

FIGURE 5-13. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis humilis*. Solid circles indicate males, hollow circles females and crosses unsexed juveniles.

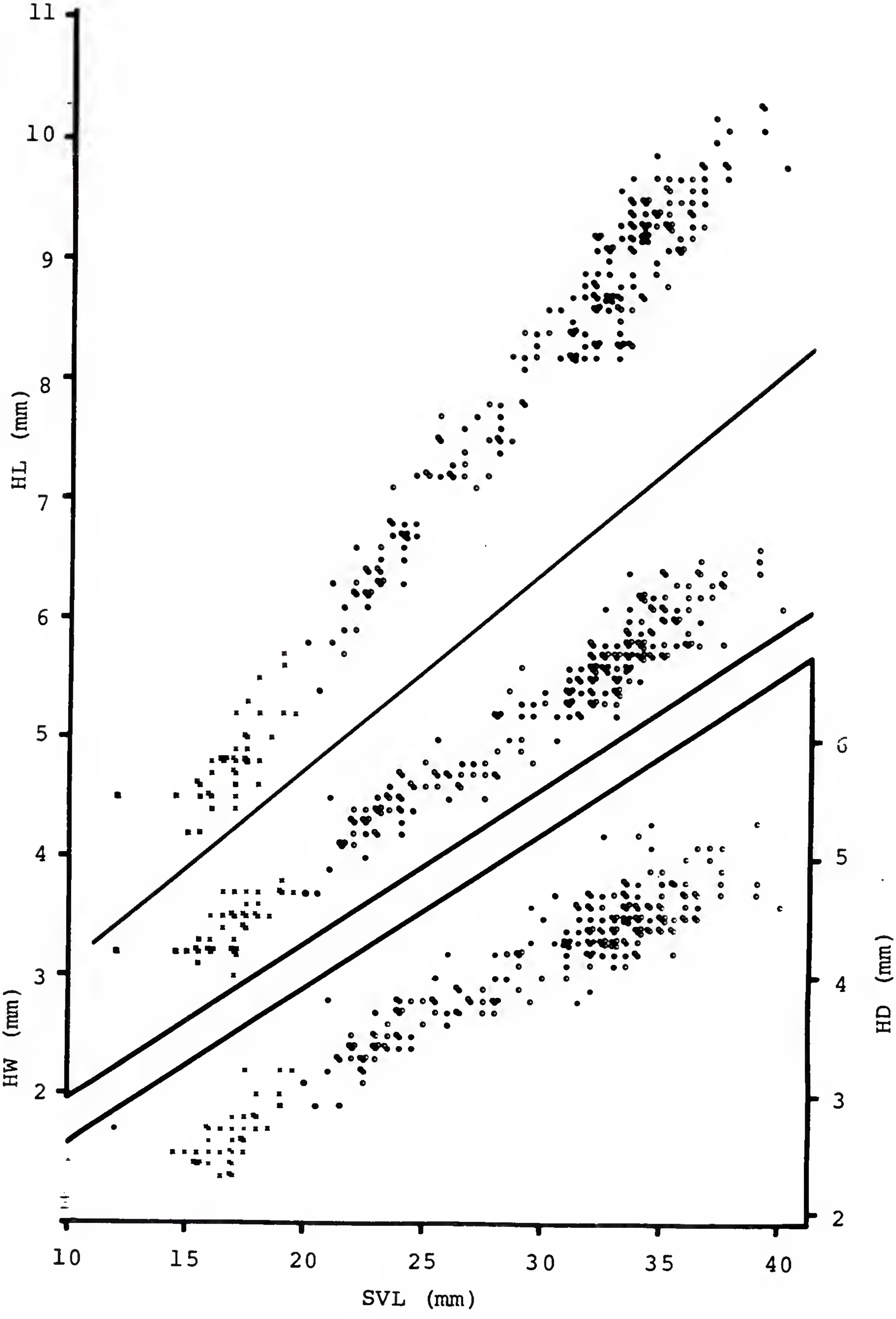

HL (mm)
HW (mm)
HD (mm)
SVL (mm)
11
10
9
8
7
6
5
4
3
2
6
5
4
3
2
10
15
20
25
30
35
40

FIGURE 5-14. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis limifrons*. Symbols as in Figure 5-13.

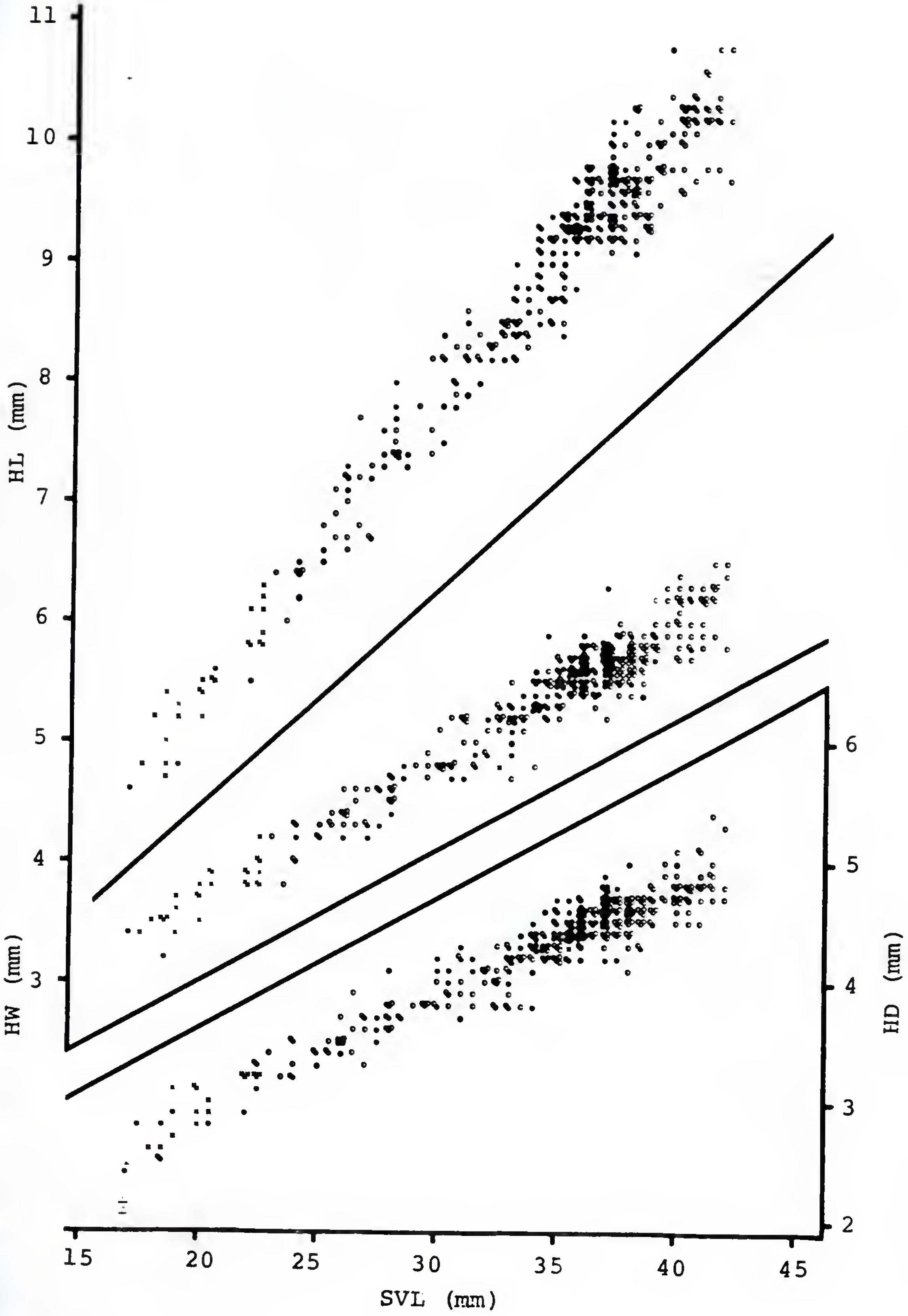

11
10
9
8
7
6
5
4
3
HL (mm)
HW (mm)
6
5
4
3
2
HD (mm)
15
20
25
30
35
40
45
SVL (mm)

FIGURE 5-15. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis carpenteri*. Symbols as in Figure 5-13.

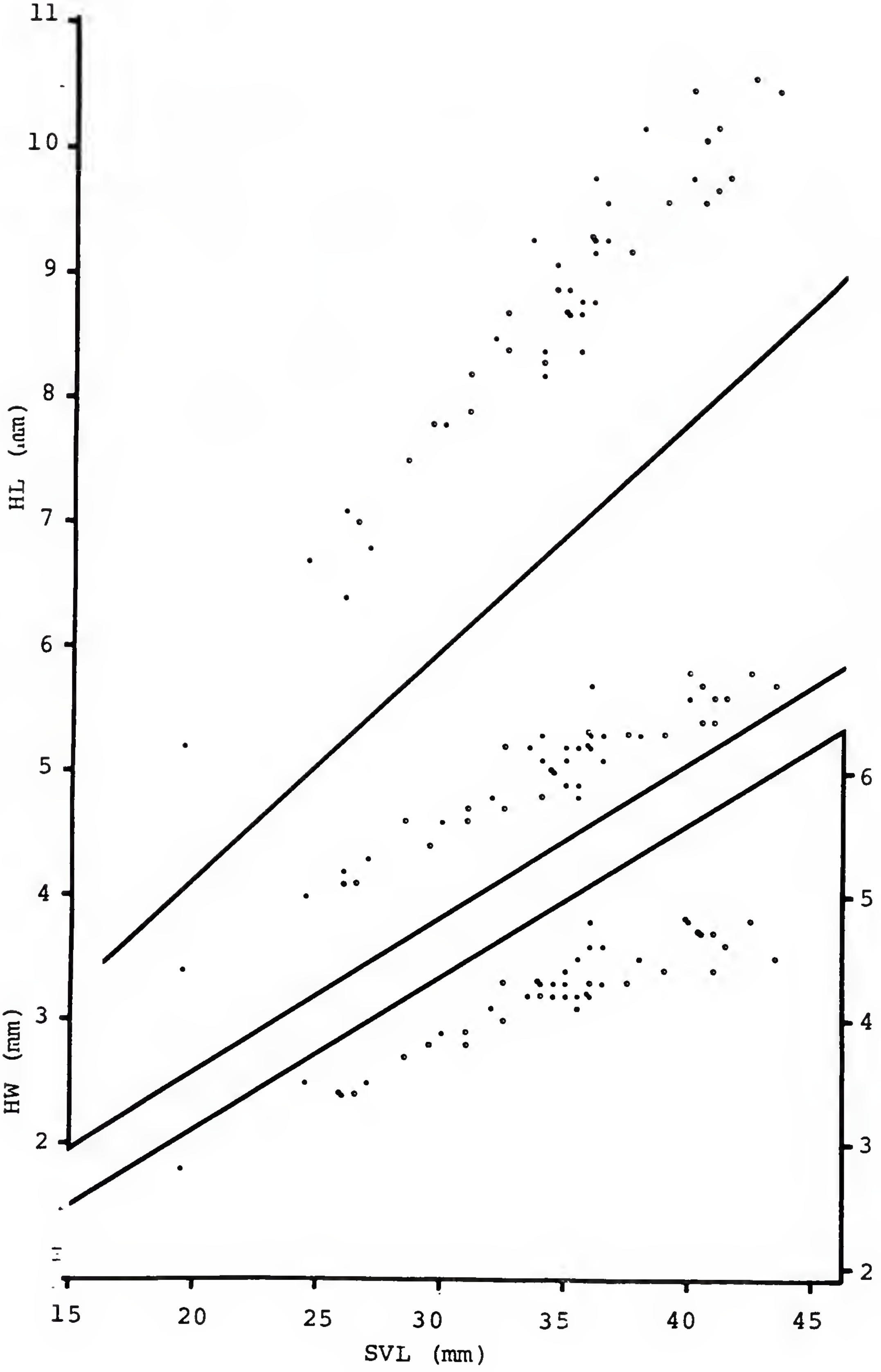

11
10
9
8
7
6
5
4
3
2
HL (mm)
HW (mm)
HD (mm)
6
5
4
3
2
15
20
25
30
35
40
45
SVL (mm)

FIGURE 5-16. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis lemurinus*. Symbols as in Figure 5-13.

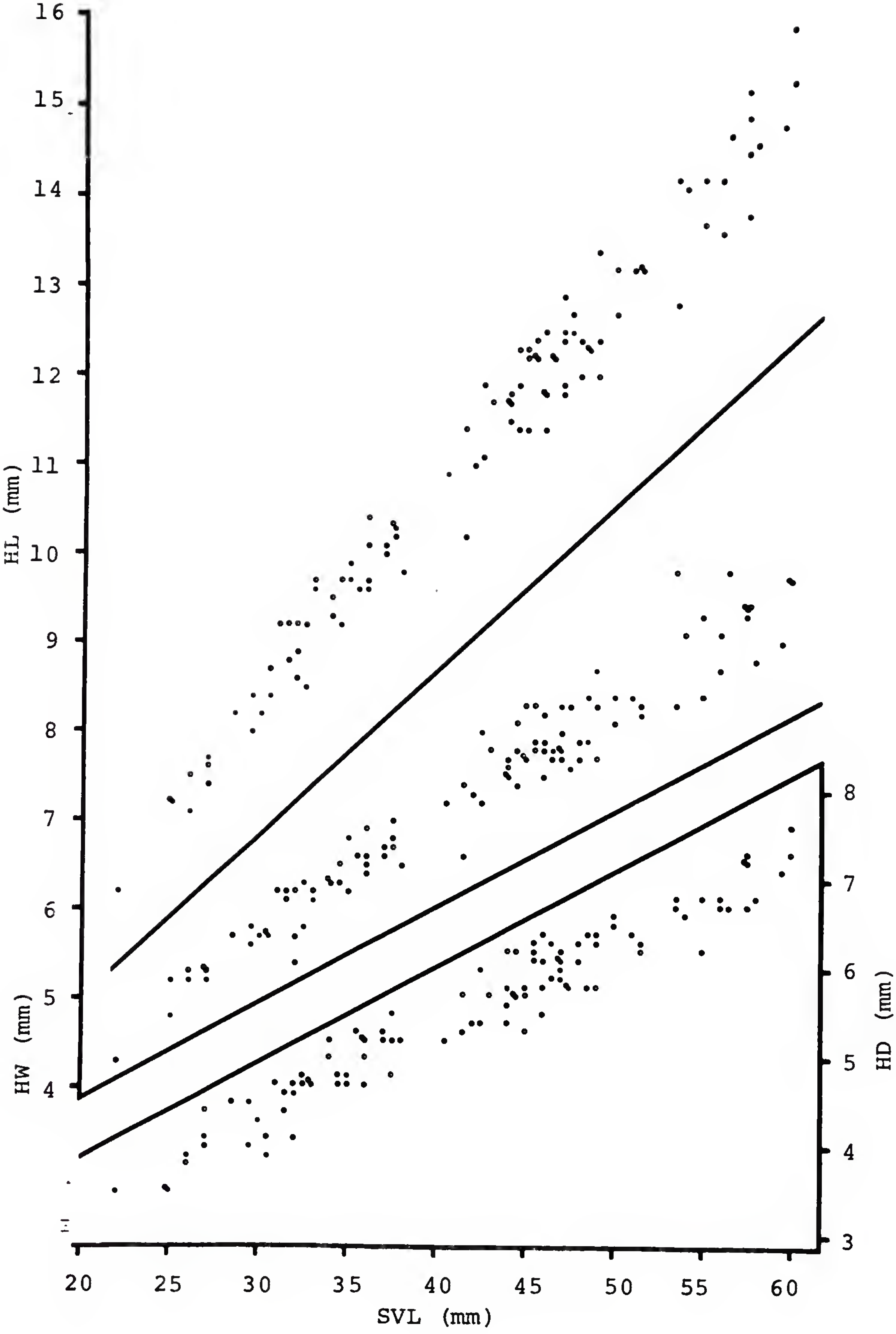

HL (mm)
16
15
14
13
12
11
10
9
8
7
6
5
4
HW (mm)
HD (mm)
8
7
6
5
4
3
SVL (mm)
20
25
30
35
40
45
50
55
60

FIGURE 5-17. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis pentaprion*. Symbols as in Figure 5-13.

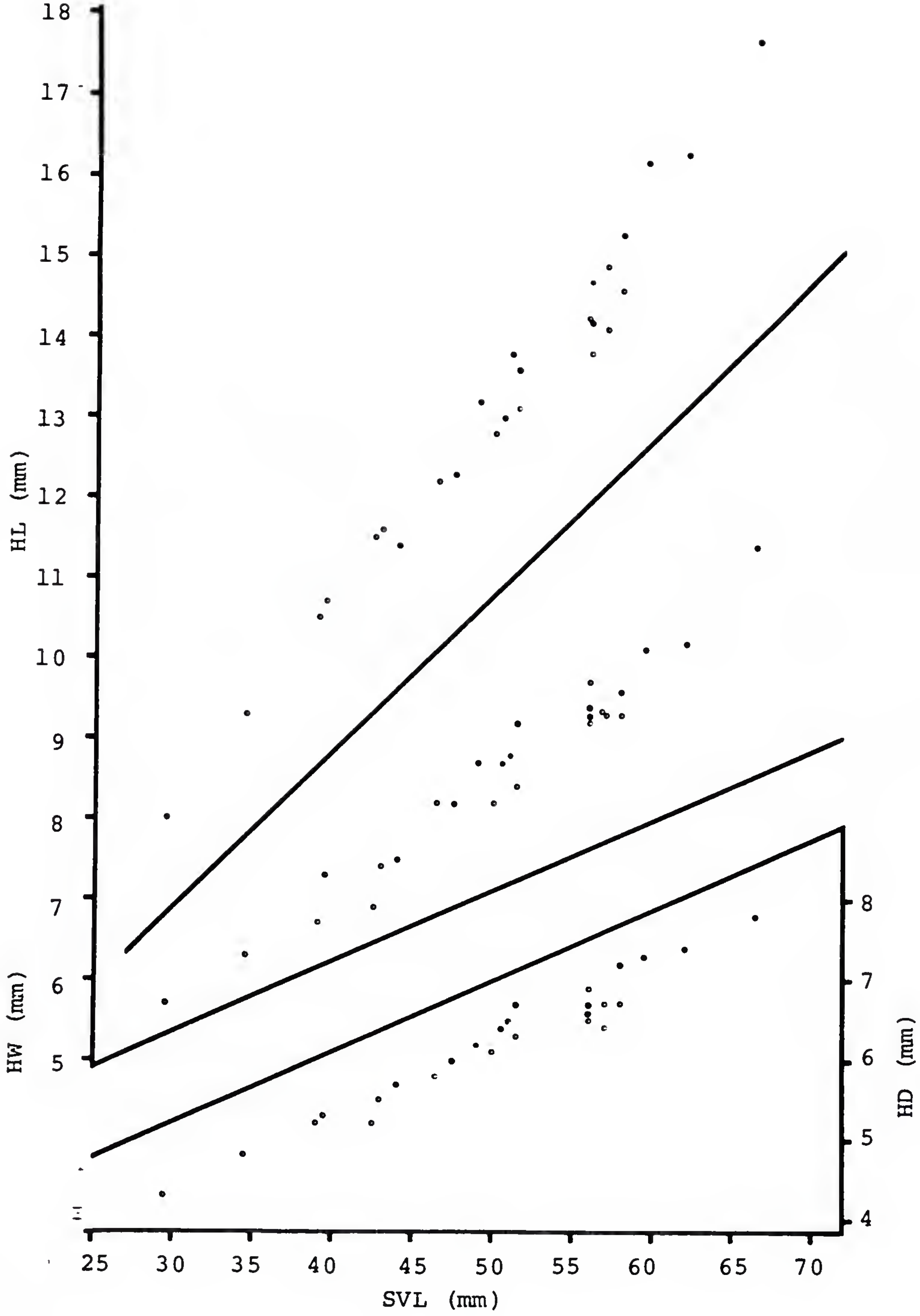

18
17
16
15
14
13
12
11
10
9
8
7
6
5
HL (mm)
HW (mm)
8
7
6
5
4
HD (mm)
25
30
35
40
45
50
55
60
65
70
SVL (mm)

FIGURE 5-18. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis lionotus*. Symbols as in Figure 5-13.

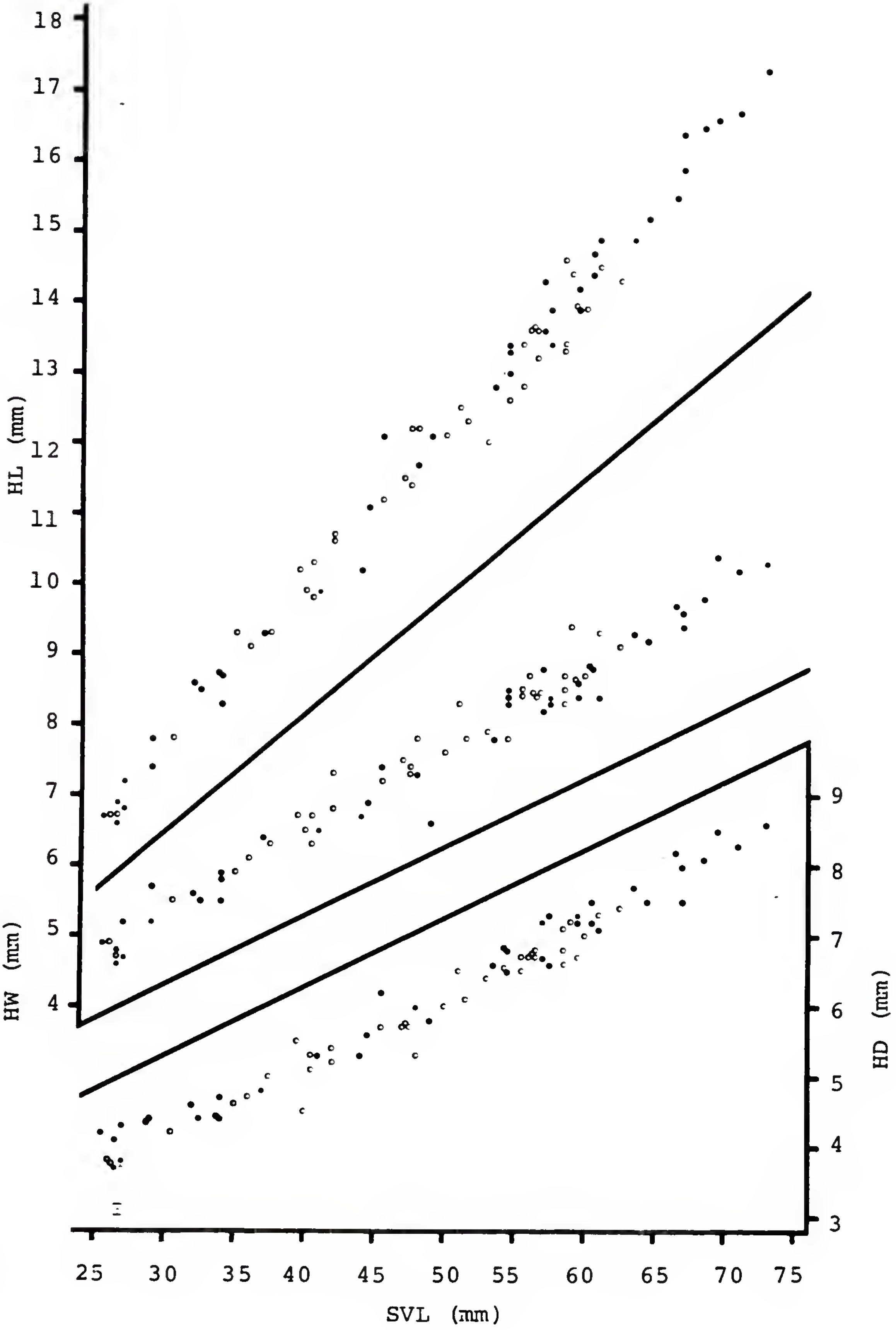

HL (mm)
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
HW (mm)
HD (mm)
9
8
7
6
5
4
3
25
30
35
40
45
50
55
60
65
70
75
SVL (mm)

FIGURE 5-19. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis capito*. Symbols as in Figure 5-13.

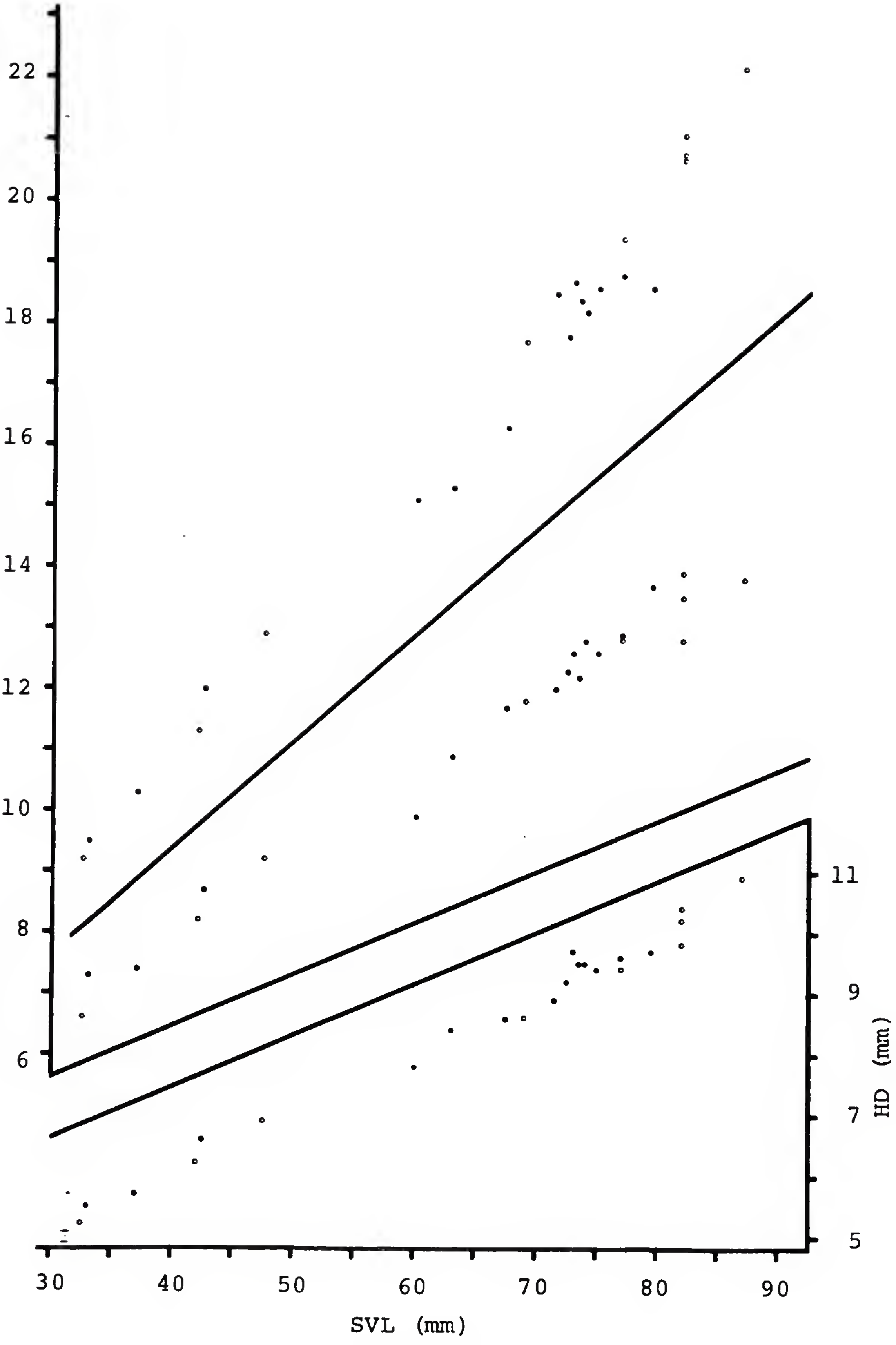

22
20
18
16
14
12
10
8
6
HL (mm)
HW (mm)
11
9
7
5
HD (mm)
30
40
50
60
70
80
90
SVL (mm)

FIGURE 5-20. Head Length (HL), Head Width (HW) and Head Depth (HD) in *Anolis biporcatus*. Symbols as in Figure 5-13.

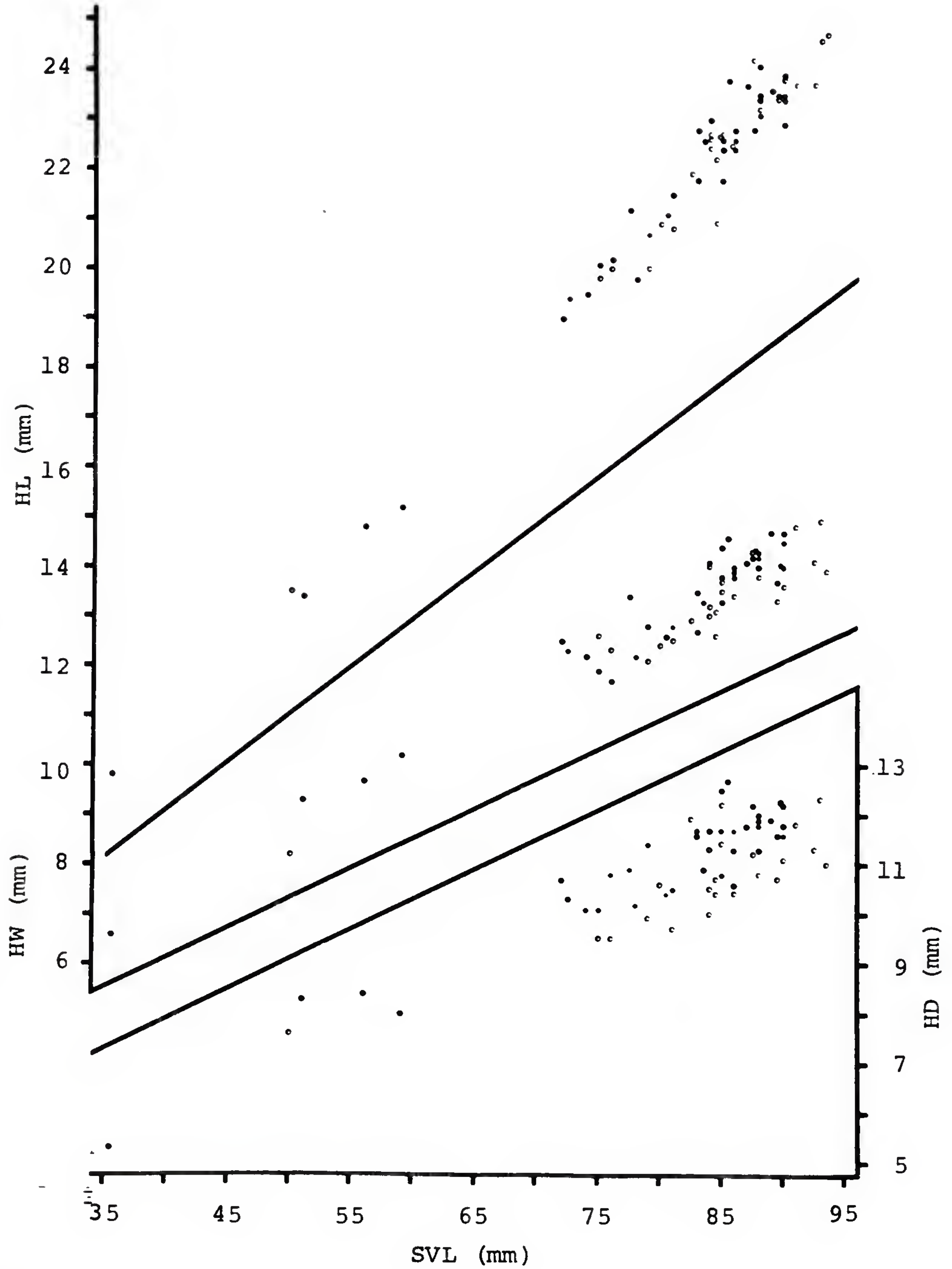

HL (mm)
24
22
20
18
16
14
12
10
8
6
HW (mm)
13
11
9
7
5
HD (mm)
35
45
55
65
75
85
95
SVL (mm)

FIGURE 5-21. Relation of Mean Prey Length to Lizard Head Length. Lines indicating the species are as follows:

A. humilis, solid, separated dots;
A. limifrons, hollow squares;
A. carpenteri, diamonds;
A. lemurinus, solid line;
A. pentaprion, hollow dots;
A. lionotus, dashed line;
A. capito, solid, connected dots; and
A. biporcatus, dot and dash line.

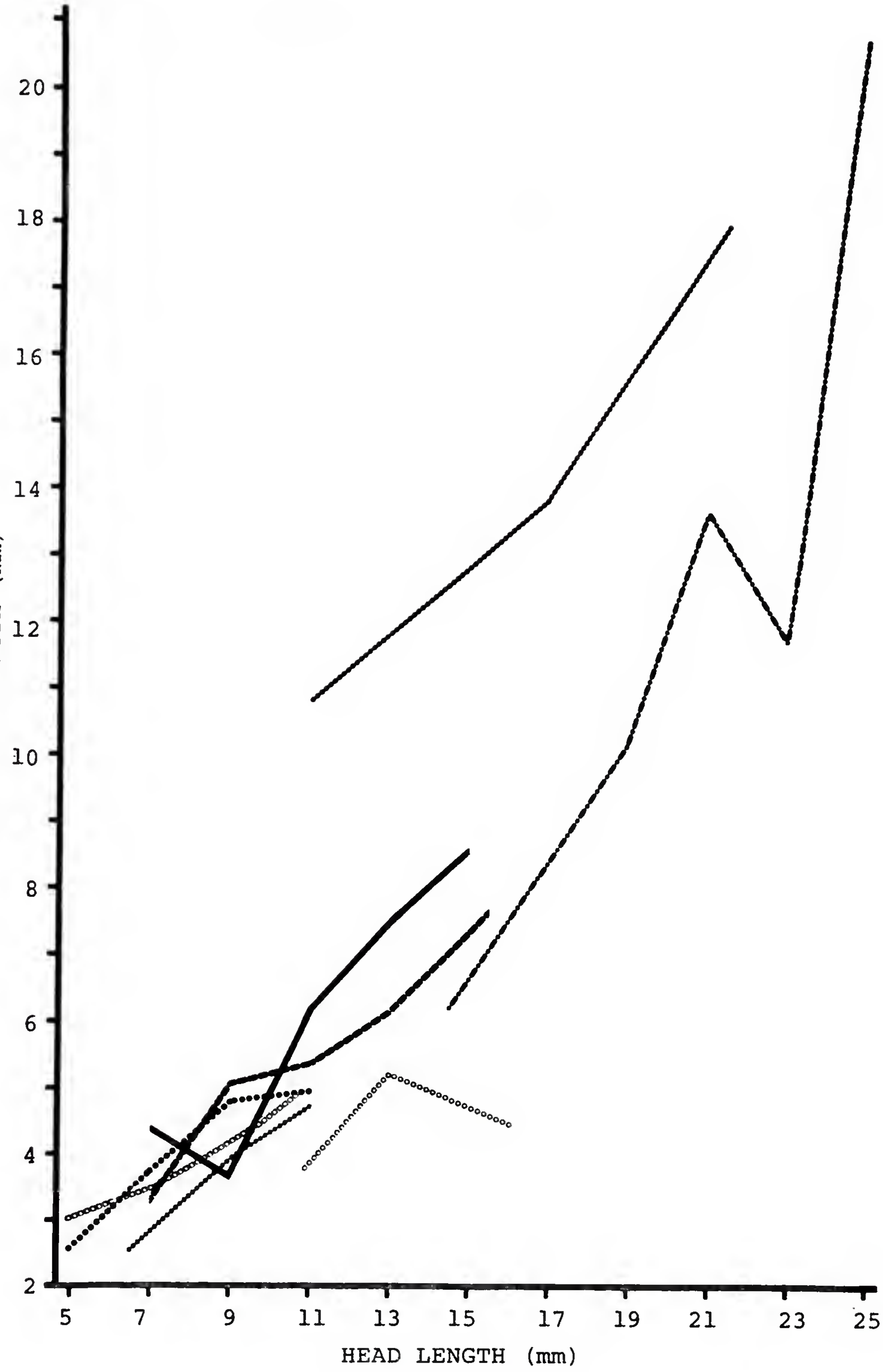
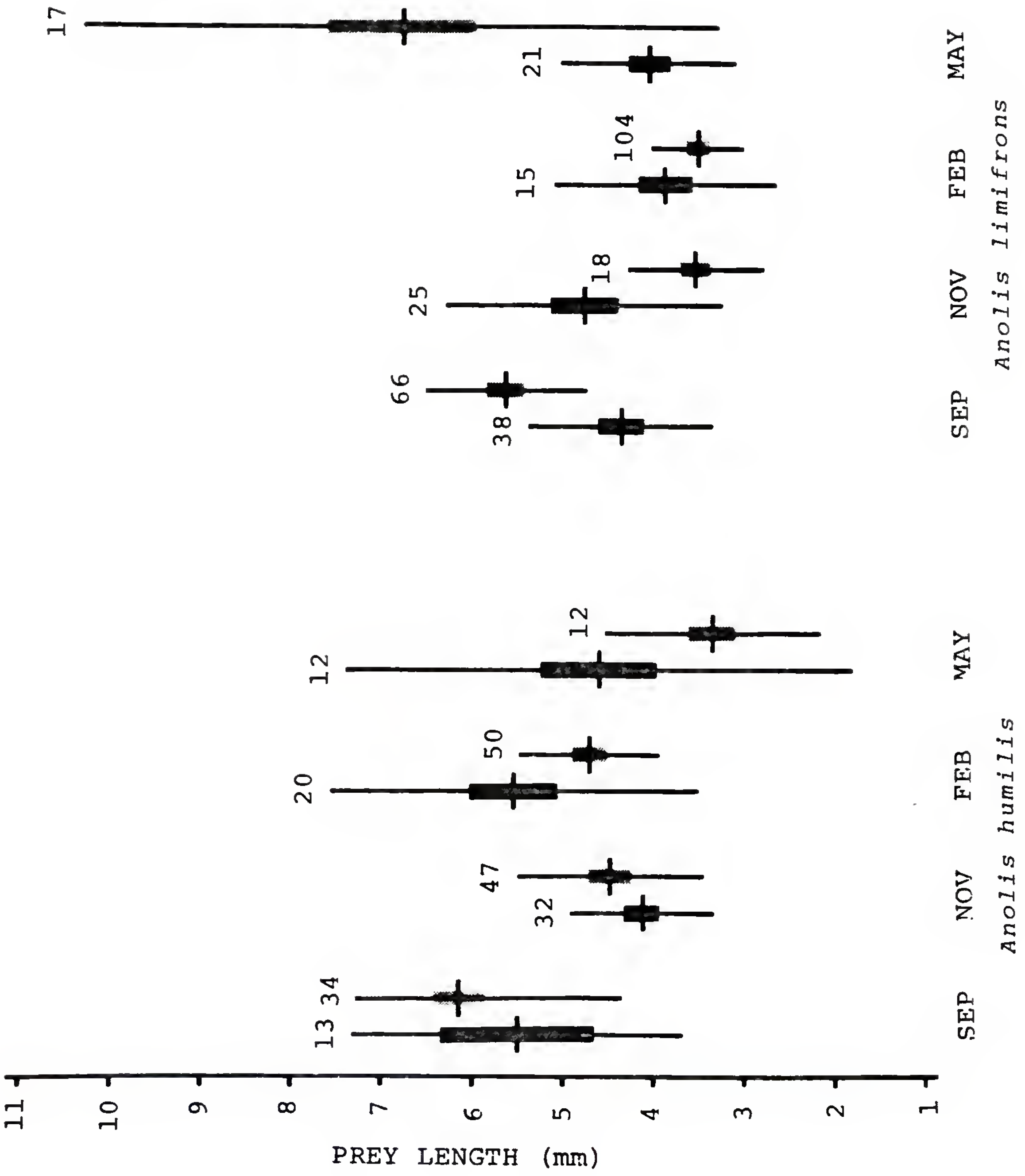
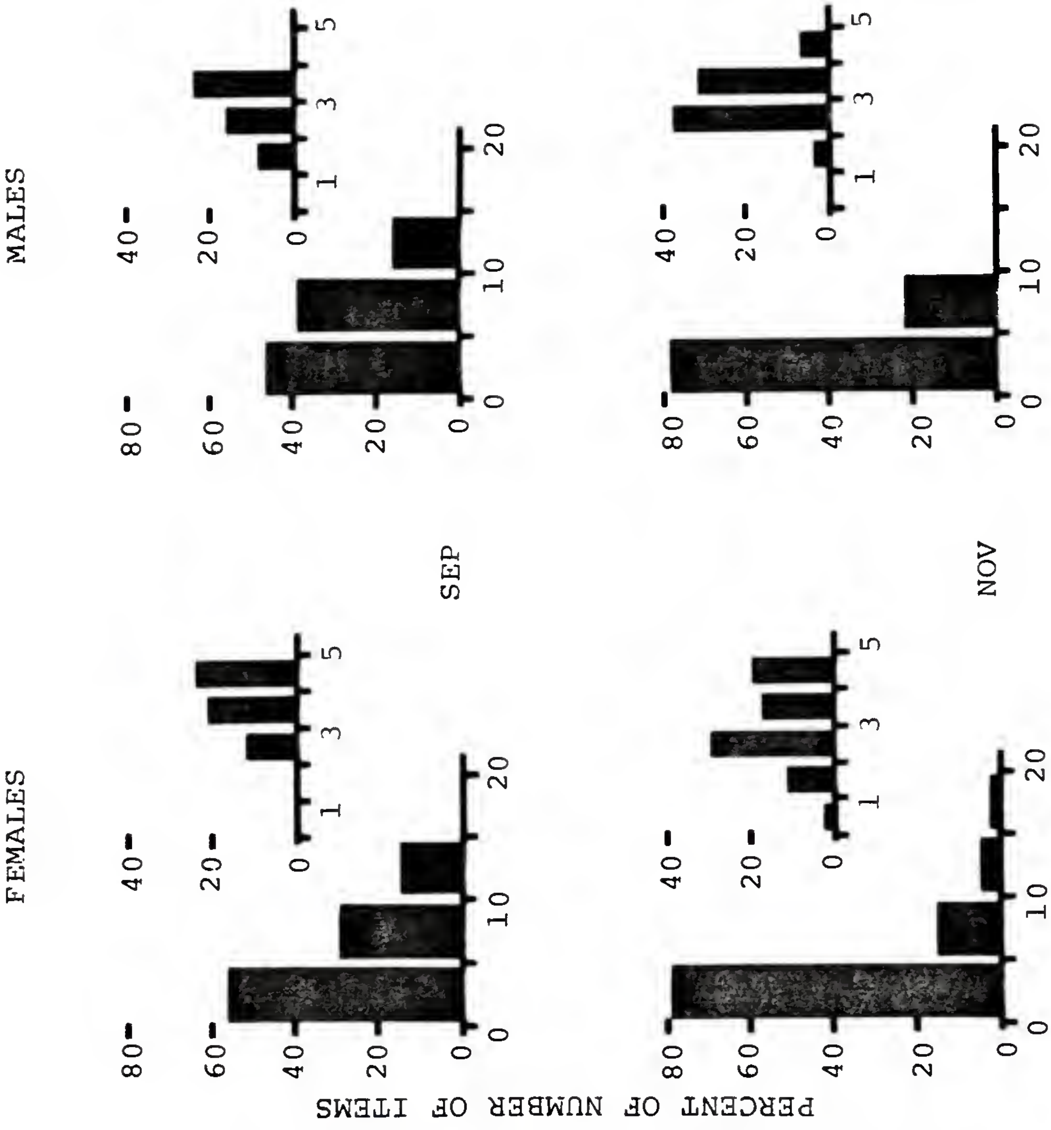

MEAN PREY LENGTH (mm)
2
4
6
8
10
12
14
16
18
20
HEAD LENGTH (mm)
5
7
9
11
13
15
17
19
21
23
25

FIGURE 5-22. Seasonal Variation if Prey Length for *Anolis humilis* and *Anolis limifrons*. For each period, long males are on the left (solid bar) and long females are on the right (stippled bar). Means are horizontal lines; vertical lines are 95% confidence intervals; and bars are on standard error. Sample sizes are indicated above the confidence intervals.


PREY LENGTH (mm)
11
10
9
8
7
6
5
4
3
2
1
SEP
NOV
FEB
MAY
Anolis humilis
13
34
32
47
20
50
12
12
SEP
NOV
FEB
MAY
Anolis limifrons
38
66
25
18
15
104
21
17


FEMALES
MALES
SEP
NOV
PERCENT OF NUMBER OF ITEMS
0
20
40
60
80
0
10
20
0
1
3
5

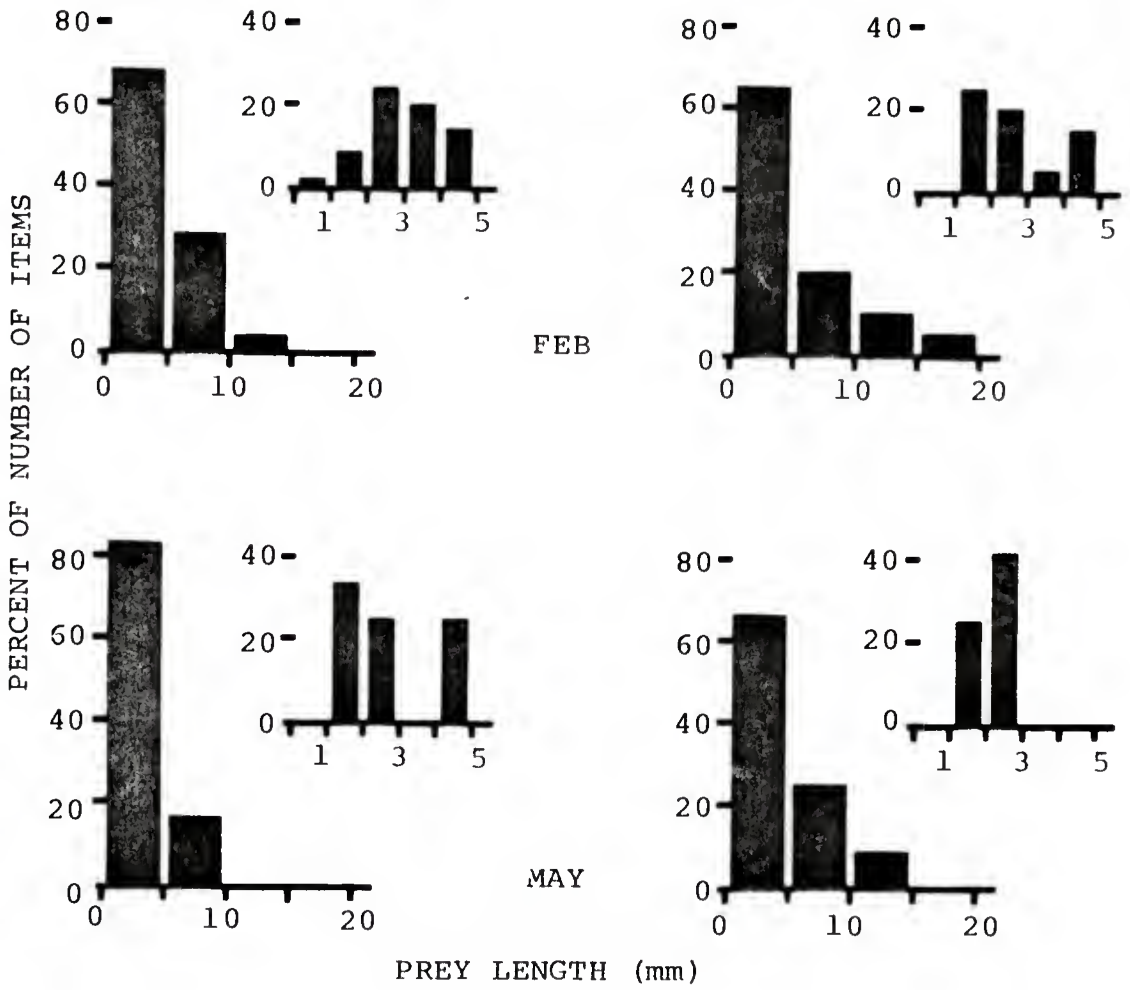
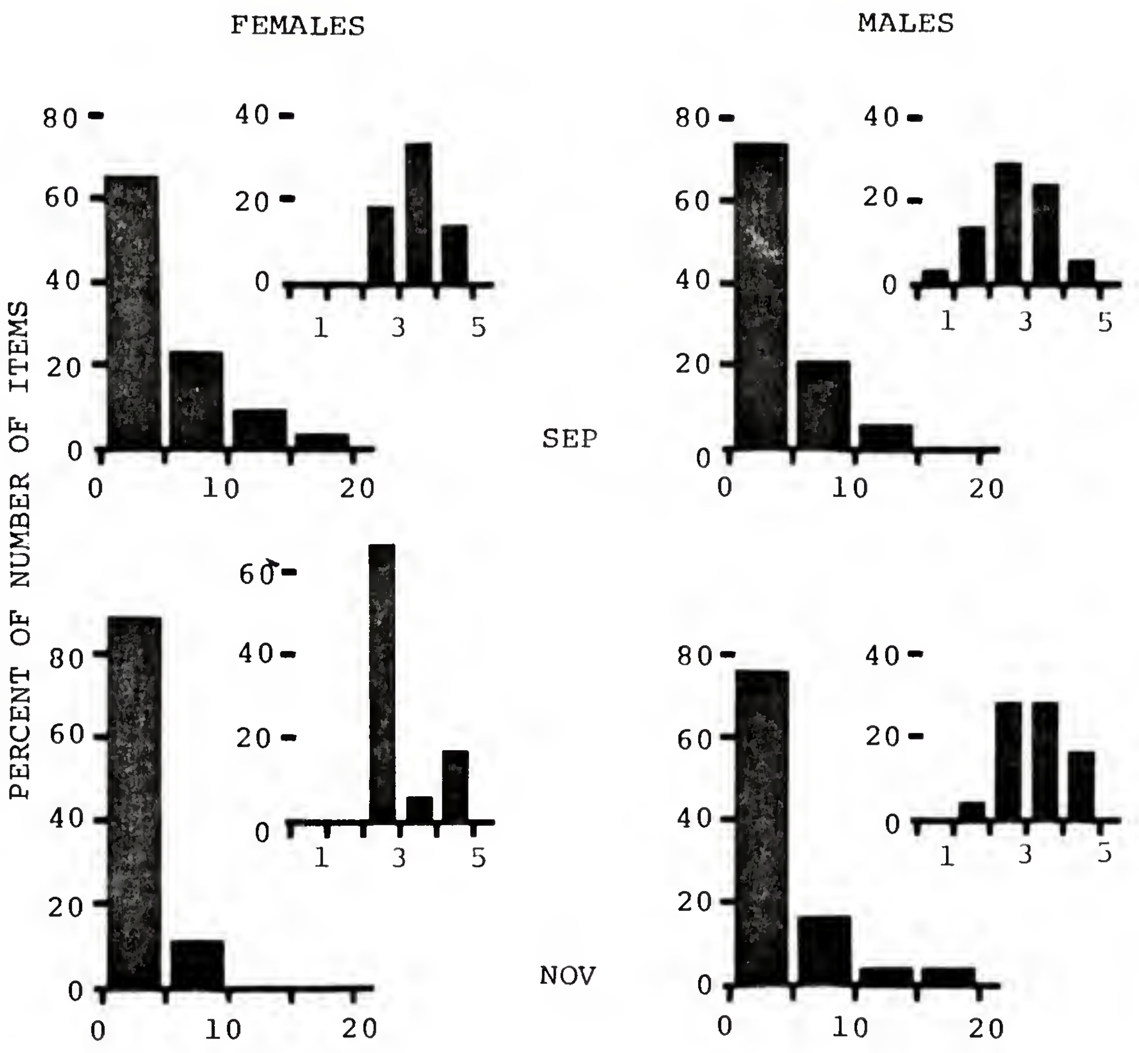


FIGURE 5-23. Seasonal Differences in Distribution of Prey by Frequency According to Prey Length for the Large *Anolis humilis*.


FEMALES
MALES
PERCENT OF NUMBER OF ITEMS
SEP
NOV
80
60
40
20
0
10
20
1
3
5

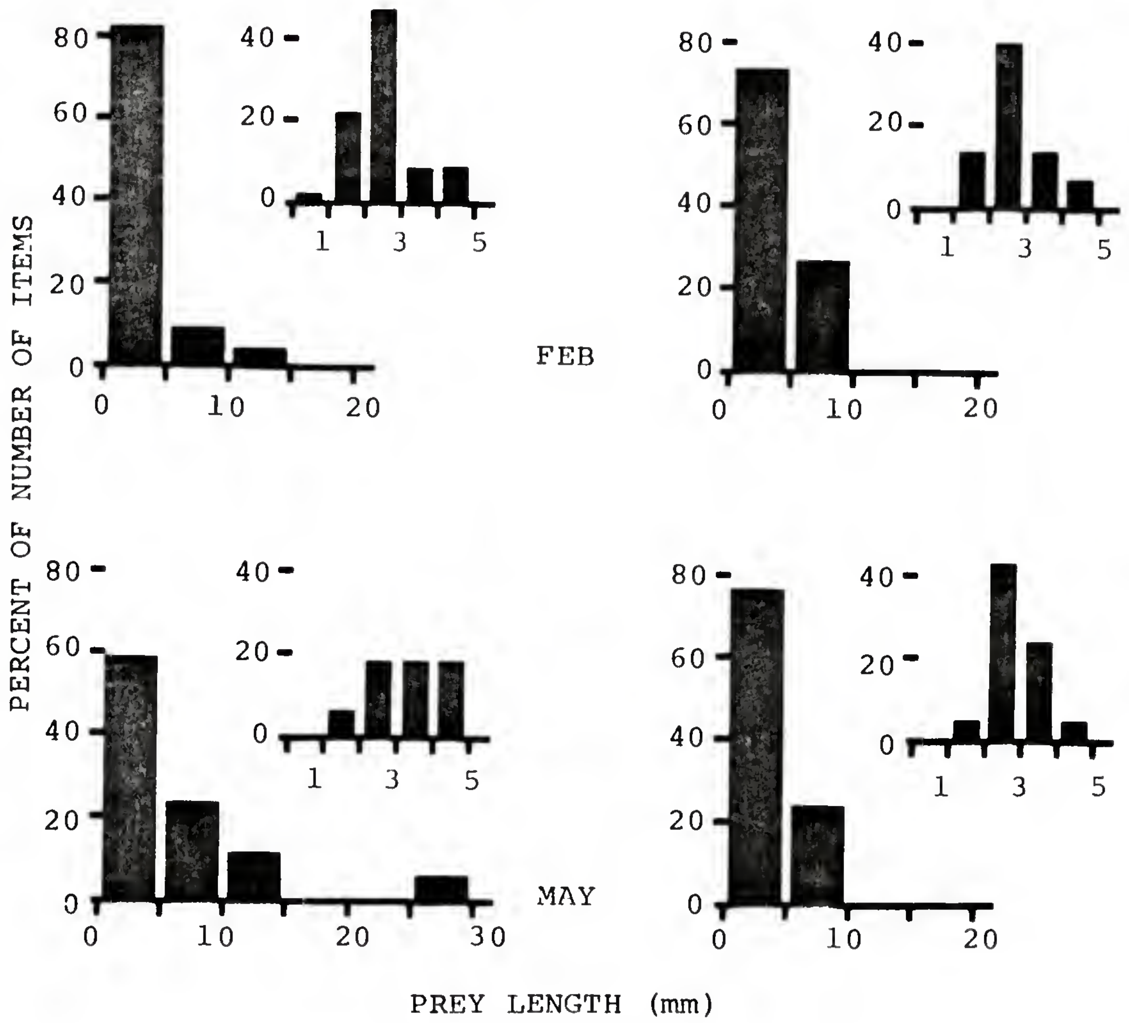


FIGURE 5-24. Seasonal Differences in Distribution of Prey by Frequency According to Prey Length for the Large *Anolis limifrons*.

FIGURE 5-25. Prey Lengths of Long Males and Long Females of Río Frío *Anolis*. Horizontal lines are mean lengths; vertical lines are 95% confidence intervals; and bars are one standard error. Sample sizes are indicated above the confidence intervals.

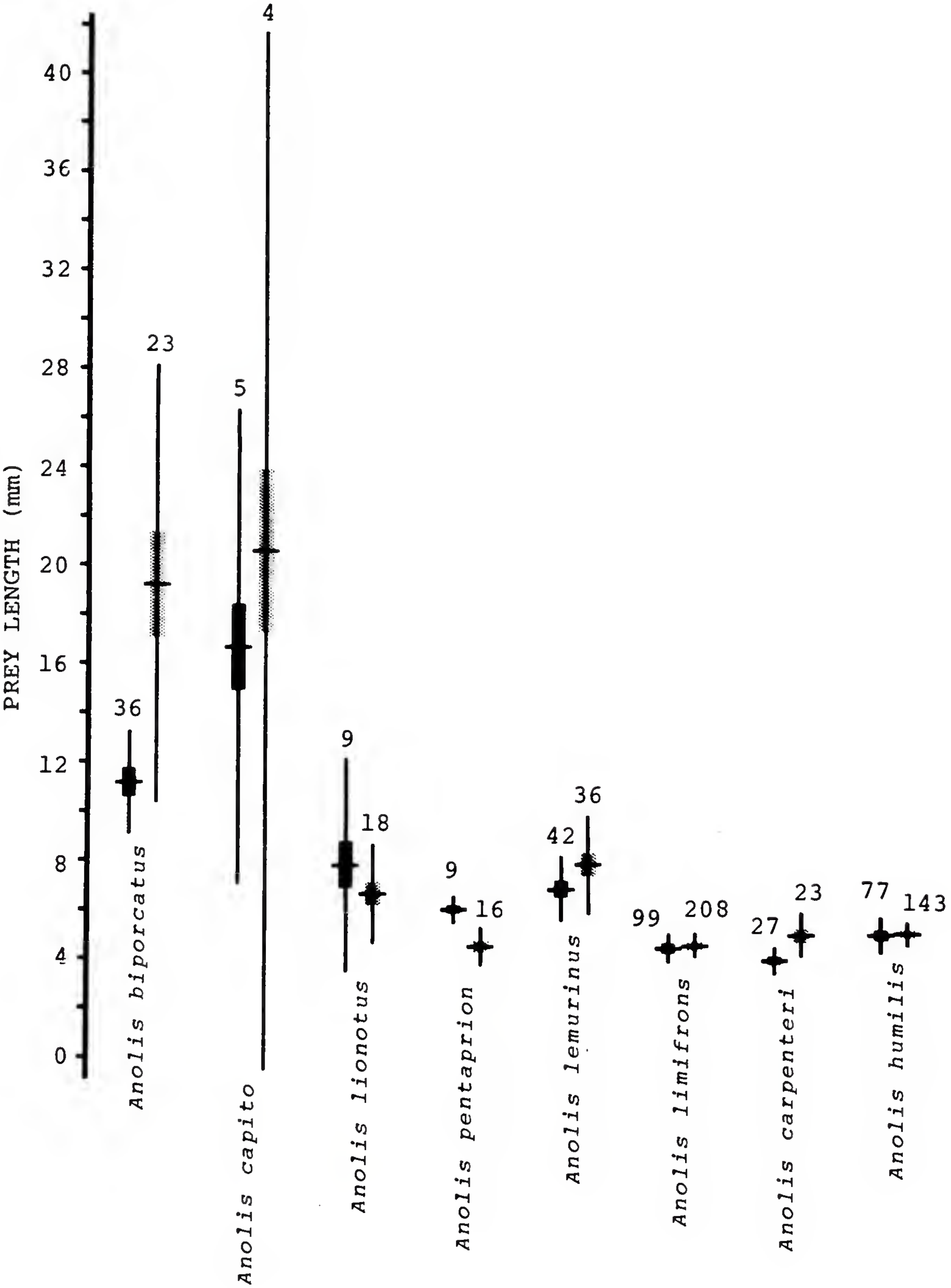

PREY LENGTH (mm)
0
4
8
12
16
20
24
28
32
36
40
36
23
5
4
9
18
9
16
42
36
99
208
27
23
77
143
Anolis biporcatus
Anolis capito
Anolis lionotus
Anolis pentaprion
Anolis lemurinus
Anolis limifrons
Anolis carpenteri
Anolis humilis

FIGURE 5-26. Size, Perch and Food of Río Frío *Anolis*. Lizard silhouettes indicate common perch sites of each species and size (.25 x SVL of long classes), males in foreground, females behind. Bar graphs indicate distributions of food of long male and long females combined. Species are indicated by:

Tree Crown - black, *A. carpenteri*
stippled, *A. pentaprion*
Trunk-Shrub - white, *A. limifrons*
black, *A. lemurinus*
stippled, *A. biporcatus*
Ground - black, *A. humilis*
stippled, *A. capito*
Streamside - black, *A. lionotus*

Circle graphs indicate the most commonly occuring prey taxa in long males and long females combined. Symbols are as shown below:

Orthoptera
Homoptera
Coleoptera
immature Lepidoptera
Diptera
Hymenoptera excluding ants
Formicidae
Isopoda
Araneida
M Miscellaneous

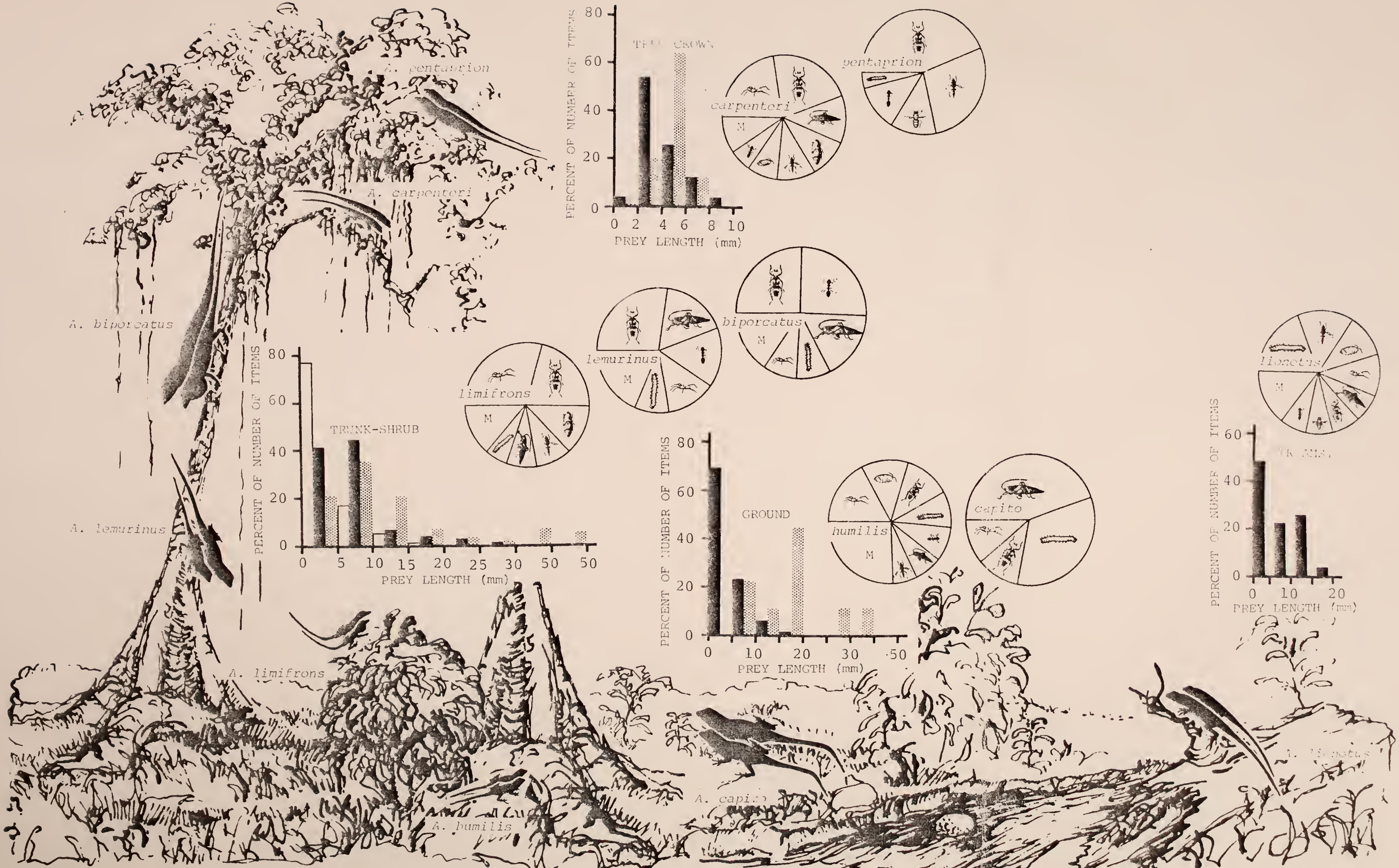

TREE CROWN
PERCENT OF NUMBER OF ITEMS
80
60
40
20
0
0 2 4 6 8 10
PREY LENGTH (mm)
carpentori
M
pentaprion
A. pentaprion
A. carpentori
A. biporcatus
A. lemurinus
A. limifrons
A. humilis
A. capito
A. lionotus
TRUNK-SHRUB
PERCENT OF NUMBER OF ITEMS
80
60
40
20
0
0 5 10 15 20 25 30 50 50
PREY LENGTH (mm)
limifrons
M
lemurinus
M
biporcatus
M
GROUND
PERCENT OF NUMBER OF ITEMS
80
60
40
20
0
0 10 20 30 ·50
PREY LENGTH (mm)
humilis
M
capito
lionotus
M
PERCENT OF NUMBER OF ITEMS
60
40
20
0
0 10 20
PREY LENGTH (mm)

FIGURE 5-27. Linear Relationship of Mean Prey Length to Lizard Head Length. Lines are least squares fitted to mean prey length in 2 mm classes. Lines are as in figure 5-21.

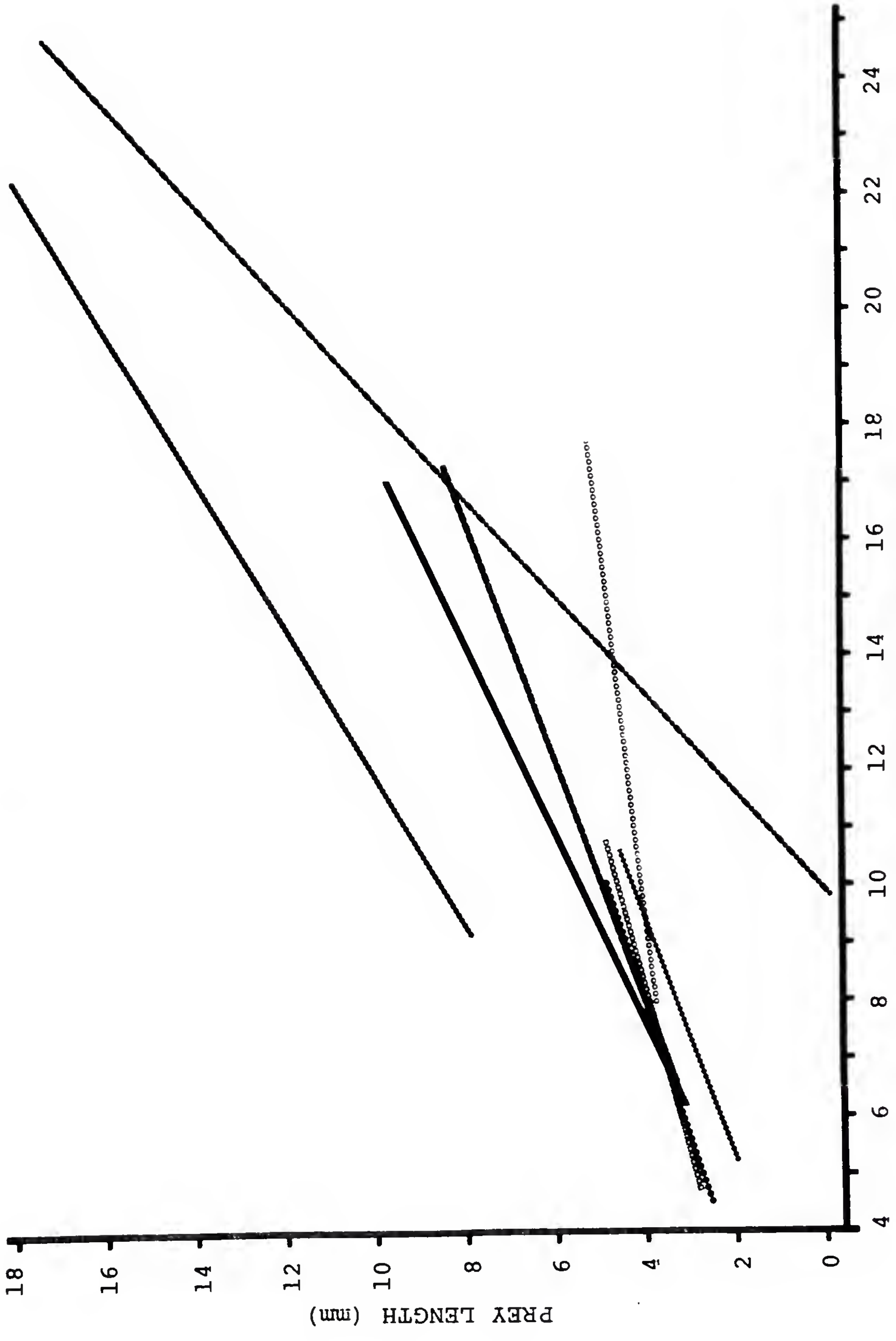

PREY LENGTH (mm)
0
2
4
6
8
10
12
14
16
18
MEAN HEAD LENGTH (mm)
4
6
8
10
12
14
16
18
20
22
24

FIGURE 5-28. Comparison of *Anolis* Food Items and Sweep Sample Arthropods by Length. Anole food (black) includes 1912 items from Río Frío anole stomachs. Sweep sample distribution is for 1600 items listed by Janzen and Schoener (1968). Arrow indicates class that includes mean prey length for all anoles, 5.32cm.

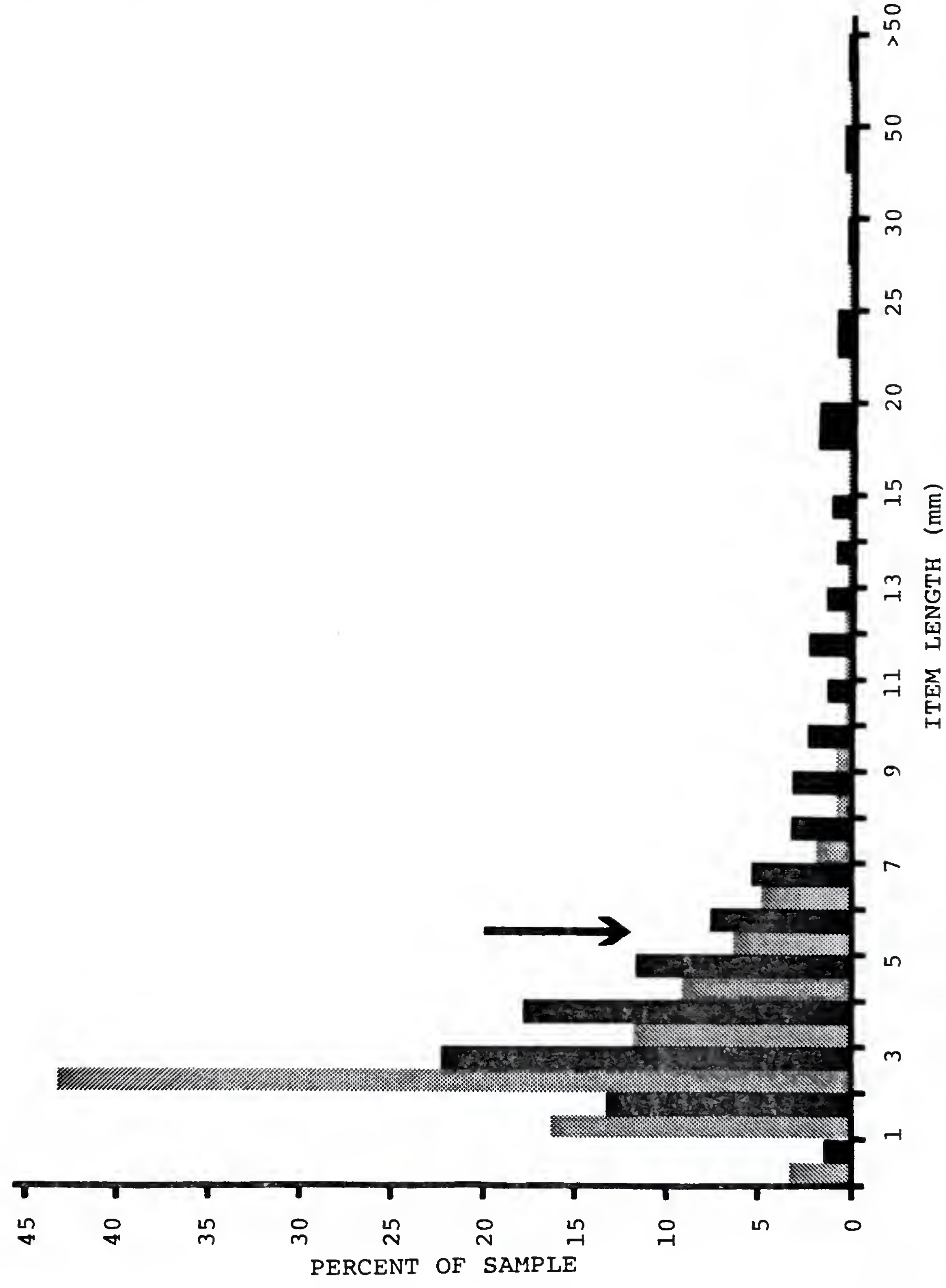

PERCENT OF SAMPLE
0
5
10
15
20
25
30
35
40
45
ITEM LENGTH (mm)
1
3
5
7
9
11
13
15
20
25
30
50
>50

FIGURE 5-29. Log Normal Distribution of Prey Sizes and Sweep Sample Arthropods. Anole food items (N=1912) are shown as the solid line. Janzen and Schoener's (1968) arthropods (N=100) are shown as a dashed line.

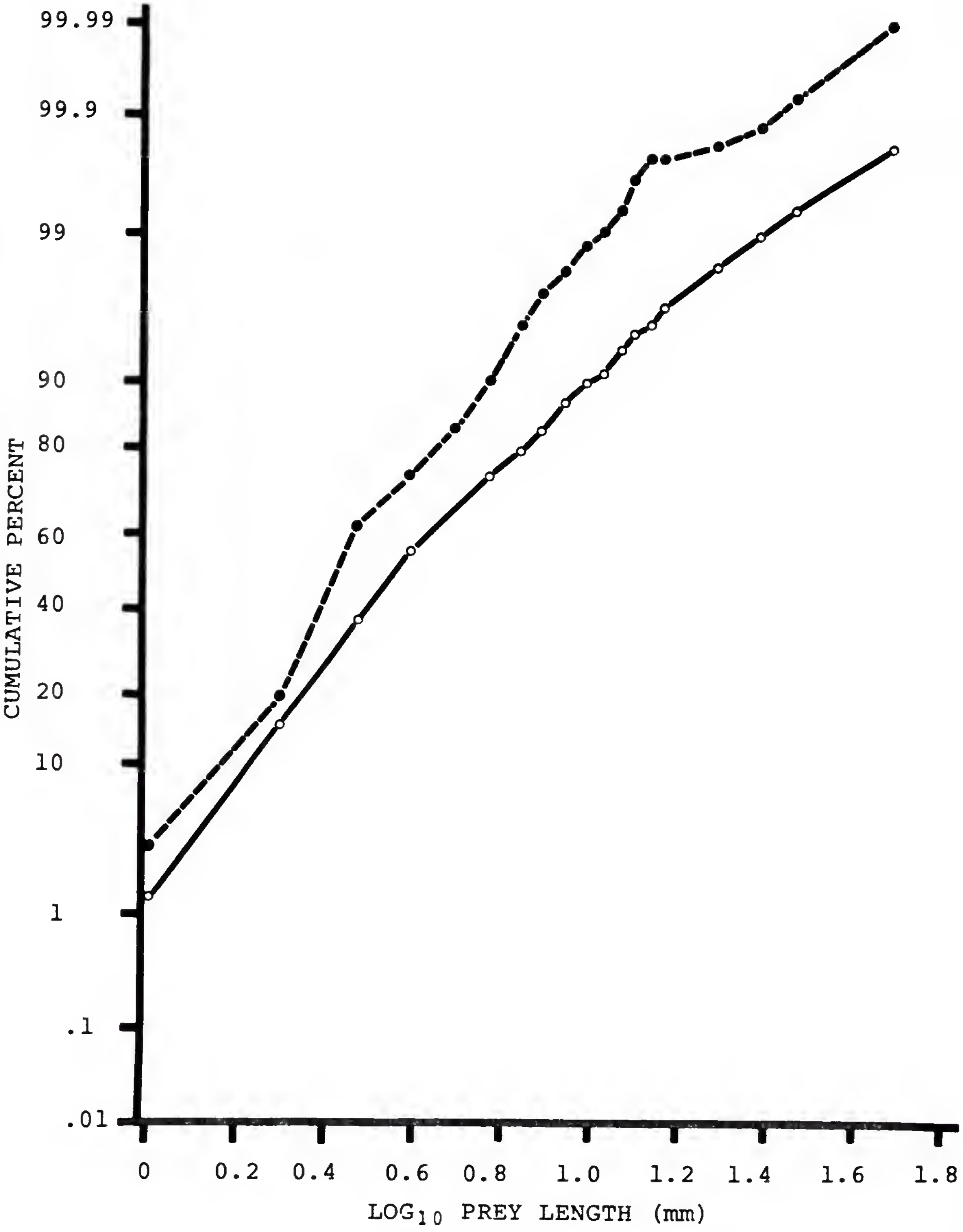

99.99
99.9
99
90
80
60
40
20
10
1
.1
.01
CUMULATIVE PERCENT
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
LOG$_{10}$ PREY LENGTH (mm)

FIGURE 5-30. Comparison of Anole Food Items and Available Prey by Taxa. Anole food (black) includes all items from Río Frío anole stomachs. Available prey distribution (stippled) is from Janzen and Schoener (1968) and Andrews (1971a); see text and table 5-2 for details of combination.

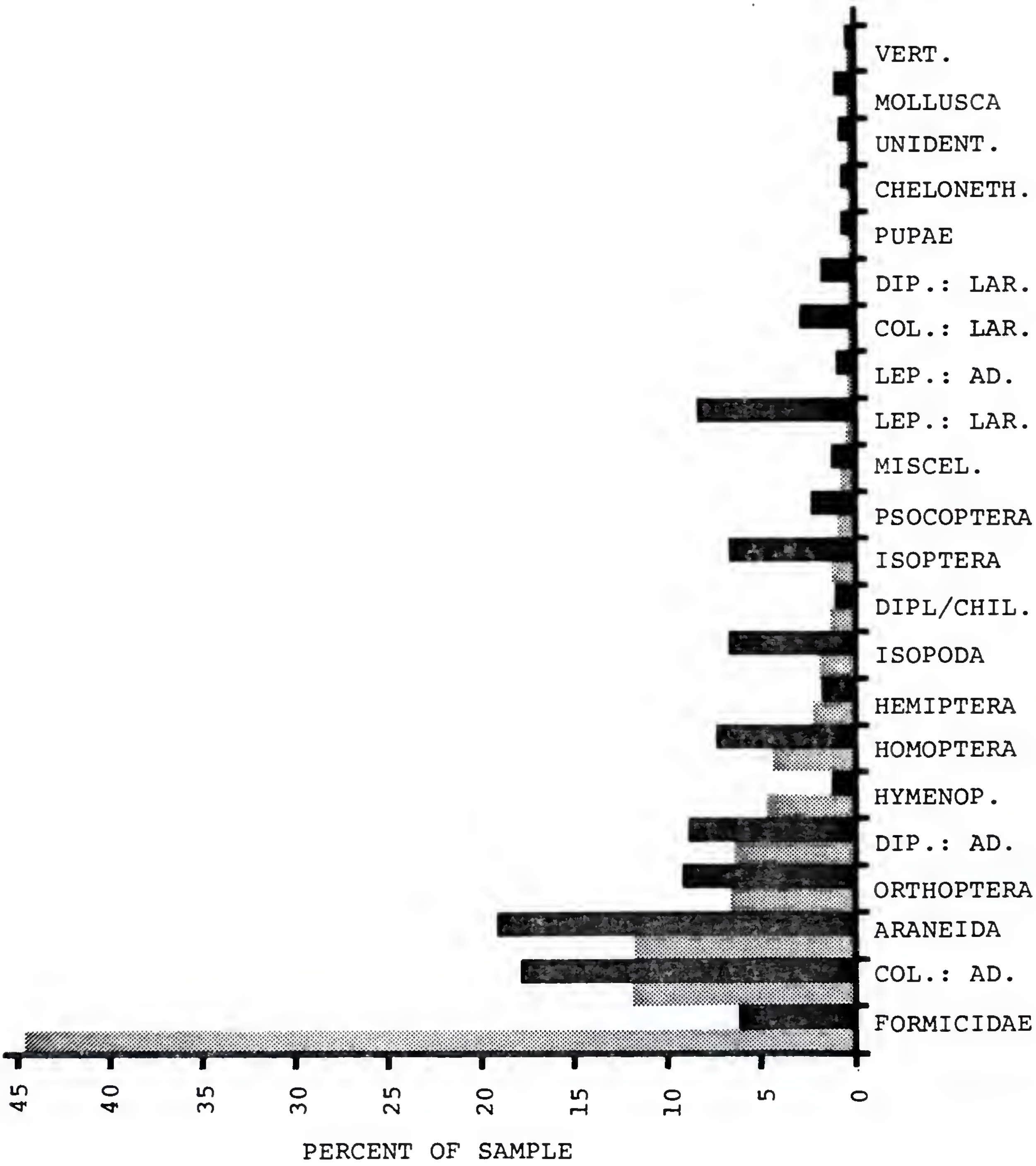
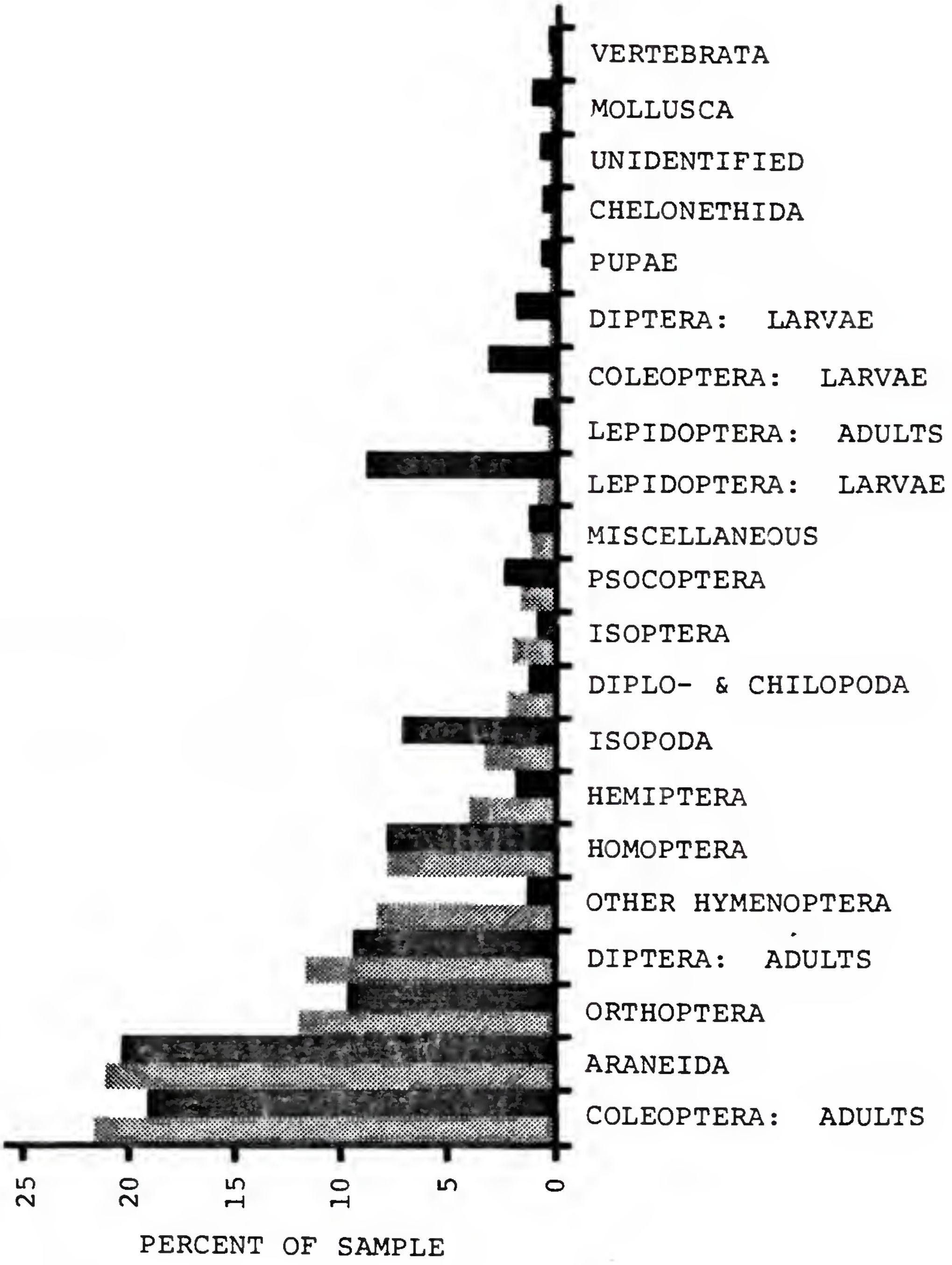

VERT.
MOLLUSCA
UNIDENT.
CHELONETH.
PUPAE
DIP.: LAR.
COL.: LAR.
LEP.: AD.
LEP.: LAR.
MISCEL.
PSOCOPTERA
ISOPTERA
DIPL/CHIL.
ISOPODA
HEMIPTERA
HOMOPTERA
HYMENOP.
DIP.: AD.
ORTHOPTERA
ARANEIDA
COL.: AD.
FORMICIDAE
45
40
35
30
25
20
15
10
5
0
PERCENT OF SAMPLE

FIGURE 5-31. Comparison of Anole Food Items and Available Prey by Taxa, Ants Excluded. Anole food (black) and available prey (stippled) are as in figure 5-30 except that ants are excluded from both.


VERTEBRATA
MOLLUSCA
UNIDENTIFIED
CHELONETHIDA
PUPAE
DIPTERA: LARVAE
COLEOPTERA: LARVAE
LEPIDOPTERA: ADULTS
LEPIDOPTERA: LARVAE
MISCELLANEOUS
PSOCOPTERA
ISOPTERA
DIPLO- & CHILOPODA
ISOPODA
HEMIPTERA
HOMOPTERA
OTHER HYMENOPTERA
DIPTERA: ADULTS
ORTHOPTERA
ARANEIDA
COLEOPTERA: ADULTS
25
20
15
10
5
0
PERCENT OF SAMPLE

VI. REPRODUCTION

1. Introduction

One of the most studied ways in which lizards respond to seasonal changes in environment concerns the timing of reproductive effort. Most tropical anoles that exhibit a seasonal change in reproductive activity have been found to have a decrease during a dry season and an increase during a wet season (Licht and Gorman, 1970; Andrews, 1971a; Sexton et al, 1971; Campbell, 1973; Fitch, 1973b; Jackson, 1973; Fleming and Hooker, 1975). Jackson (1973) found a suggestion of not only a decrease in young during the main dry season, but also during a *veranillo*, or little dry season, in a Honduran highland anole.

Experimental evidence is also available to indicate that, in at least one species, moisture is the primary cue for female reproductivity. Brown and Sexton (1973) subjected female *A. sagrei* from Belize, British Honduras, to a very low (<25%) relative humidity or to very high (>90%), both under constant photothermal conditions. Females kept dry soon became non-reproductive or remained non-reproductive, while those in moist terraria remained reproductive or soon initiated egg production. In another set of experiments, they found no effect on female reproductive state under a variety of photoperiod and temperature regimes, all with low moisture. This would seem convincing evidence that rainfall is the determining factor in regulating anole reproduction, but other experimental and field studies have suggested alternate hypotheses.

Gorman and Licht (1974) suggested that the major environmental cue to female Caribbean anoles is not rainfall, but temperature. In several species of Puerto Rican anoles, they found that egg production diminished as soon as mean air temperatures began to drop, even if this occured before any decrease in rainfall. Even where rainfall patterns were similar, upland populations had a more pronounced seasonal decline in reproductivity than did populations in the less thermally variable lowlands. Photoperiod was also thought to be involved, as it obviously influences the daily heat budget of a poikilotherm. But, because there is no altitudinal difference in day length, this was probably not a factor. Their findings are consistent with Licht's evidence for photothermal control of testicular regression in *A. carolinensis* (Licht, 1967a, 1967b, 1971) and of ovarian cycle in *A. carolinensis* and *A. sagrei* (Licht, 1973).

Of the few Costa Rican anoles studied previously, only three species reported by Fitch (1973a, b) are found in the Caribbean lowlands. He suggested that *A. humilis* and *A. lionotus* probably breed year round, with some reduction during the dry season, and that *A. limifrons* is also reproductive all year, but possibly with a more pronounced decrease in the dry season.

To determine the extent of seasonality and the predominant environmental cue, I determined reproductive activity during the four collecting periods. These periods are quite distinct with regard to temperature, photoperiod and rainfall (Table 6-1). The September period is during the *veranillo*, a "little dry season" that usually occurs from late July through September, photoperiod is decreasing, and daily maximum temperatures are still high. By November, the *veranillo* is over and rainfall is high, daylength is almost at its shortest, and temperatures are low. As discussed earlier, February 1970 was exceptionally rainy. In a normal year February would be the driest month, with an increasing photoperiod and low temperatures. May, at the beginning of the wet season, usually has high rainfall, almost maximal daylength and high temperatures, although May of 1970 had slightly less than average rainfall. These differences should allow some inferences to be made about the causes of seasonal fluctuations in reproductivity of Río Frío anoles.

2. Materials and Methods

Anoles were collected, measured and preserved as has been described in preceding sections. Reproductive condition was determined and measurements taken after the lizards had been stored in alcohol.

Females.

More than 300 female *Anolis* were dissected and examined for reproductive condition. From each of these female anoles, the paired abdominal fat bodies were removed, blotted dry and weighed to the nearest 1.0 mg on a Mettler analytical balance. The length and diameters of eggs in the oviducts were measured to the nearest 0.1 mm with vernier calipers. Diameters of the largest ovarian follicle on each side were measured with an ocular micrometer, also to the nearest 0.1 mm, and their colors were noted.

In *Anolis*, a distinctive ovulatory pattern is apparently found in all species. In this well-known pattern (Cagle, 1948; Hamlett, 1952), a single egg is ovulated from one ovary and as it passes down the oviduct of the same side, a follicle is enlarging in the ovary on the opposite side. This alternation of ovaries to produce multiple single-egg clutches has been termed monoallochronic by Smith et al. (1972). Thus there are only four reproductive categories to be expected in female anoles (Licht and Gorman, 1970; Sexton et al., 1971; Gorman and Licht, 1974):

I. nonreproductive - no enlarged, yolky follicles; no oviducal eggs

II. reproductive - an enlarged, yolky follicle on one side; no oviducal eggs

III. reproductive (gravid) - an oviducal egg on one side; an enlarged, yolky follicle on the other side

IV. reproductive (gravid) - both an oviducal egg and an enlarged, yolky follicle on one side; a smaller oviducal egg on the other side

For each species, the shortest female in class II was determined. In the two species with large samples (*humilis* and *limifrons*) only individuals that were 1 mm or more longer than the shortest class III or IV were used, but in all other species any female as long or longer than the shortest class III was used. This is to assure that all specimens used had reached a minimum reproductive size. Where adequate samples were available (*A. humilis* and *A. limifrons*), there is little variation in mean SVL (Table 6-2) from period to period.

Males.

Paired abdominal fat bodies were removed and weighed as was described for females. The left testis was removed from most males, weighed to the nearest 1.0 mg, and measured (length and diameter) to the nearest 0.1 mm. The right testis and a portion of the epididymis were squashed, stained with methylene blue and examined for presence or absence of mature sperm.

In females, reproductive maturity is relatively clear, i.e. an enlarging follicle is a clear indication that an egg soon will be deposited. In males, however, testis begin to enlarge and sperm are produced at a relatively early age. Testis size is clearly correlated to body size so care must be taken that interseasonal comparisons of testis size are not really comparisons of body size. In all four periods the correlation between body size and testis weight was significant (P<.01) in both *A. humilis* and *A. limifrons*. In order to eliminate body size as a consideration, only the larger males were used, even though many smaller males had enlarged testis and mature sperm. In the selected samples of *A. humilis* and *A. limifrons* SVL varied little from period to period (Table 6-3), and there was significant correlation between SVL and testis weight only in the NOV *A. humilis* ($P<.05$) and MAY *A. limifrons* ($P<.01$). Licht and Gorman (1970) also found testis size affected by body size, and minimized this by using only large males.

The use of large males also minimizes the effect of body size on fat body size. In both *A. humilis* and *A. limifrons*, fat body size is significantly correlated to body size in two of four periods. When only the large males in the reproduction samples are considered, however, there is no significant correlation in either species in any period.

3. Results for *Anolis humilis*

The smallest anole at Río Frío is also one of the two most abundant (See section VII), so adequate samples are available from all four collecting periods. The smallest reproductive female, i.e. at least class II, was 31 mm SVL, so all females with SVL of 32 mm or greater were used. Testis enlarge as male *A. humilis* grow. Linear regression of testis weight on SVL for all 98 males is significant ($r=0.86$, $P<.01$), with a least squares slope of 0.86 mg/mm. Sperm are present in most males greater than 23 mm SVL and abundant in all greater than 26 mm. As Fitch (1956) has pointed out, however, gamete production is not necessarily an indication of breeding activity, so no male of less than 30.5 mm SVL was used.

Females.

All female *A. humilis* were reproductive in September, November and May samples; and the sample collected during February, normally the driest month of the year still had 90% of the females reproductive (Fig. 6-1). If only gravid females, classes III and IV, were considered, it is apparent that, in addition to a February reduction, there is a decline in gravidity during the *veranillo*. In both September and February about 75% were gravid, compared to 83% in November and 94% in May. Yet when adjacent periods are compared, i.e. SEP vs. NOV, NOV vs. FEB, FEB vs. MAY, these are not significant differences ($P>.05$, 2 x 2 chi-squared test comparing the number gravid, classes III and IV, and the number not gravid, classes I and II).

If the September (*veranillo*) and February (dry season) samples are combined and compared with a combined November and May (wet season) sample, the proportion gravid is not significantly different (Table 6-4). Nor is there an obvious temperature effect. When the two warmer periods, September and May are combined and compared with the two cooler periods, November and February, no significant difference is seen.

These results are in general agreement with the observations of Fitch (1973b) at several Costa Rican sites. For this species he noted that "nearly all adult females appear to be gravid regardless of time of year" but that "the rate of reproduction is somewhat slackened during the early months of the calendar year."

In addition to changing the proportion of females gravid, seasonal environmental differences might cause a change in the actual rate of egg production by individual females. This possibility was discussed by Andrews (1971a) for *A. polyepis* and *A. carolinensis*. She pointed out that if the length of time it takes for an egg to traverse the oviduct is constant[1], the frequency of two oviducal eggs will increase as the rate of egg production increases (Fig. 6-2). When the number of females with one egg and the number with two eggs are compared for adjacent periods, the differences are not significant ($P>.05$, 2 x 2 chi-squared test). Nor is the difference in egg production rate significant if a combined dry season (September and February) sample is compared to a combined wet season (November and May) sample; or if a combined cool season (November and February) sample is compared to a combined warm season (September and May) sample (Table 6-4). In short, it seems that though variation in female reproductivity is apparent, it is neither statistically significant nor clearly attributable to temperature or rainfall.

---

[1] This assumption may not always be tenable. Fitch (1973b) suggested that eggs may develop weeks before they are to be deposited and held in oviducts until suitable environmental conditions prevail. Also, Henderson's (1972) report of an *A. biporcatus* depositing two eggs nearly simultaneously indicates that an egg may remain in one oviduct longer than one in the contralateral oviduct. This may have been caused by the lizards not finding an appropriate oviposition site for the older egg. Whatever the cause, this seems an isolated incident; McCoy (1975) indicated that deposition of two eggs at a time is not usual for *A. biporcatus*. It seems that regularly alternating oviposition and, therefore, regularly paced ovidcut traversals are the rule in anoles.

There is one possible reflection of egg production that does show a significant variation. When the numbers of juveniles (SVL<20 mm) are compared to the numbers of larger *A. humilis*, there is significant variation among the seasons ($P<.05$, 2 x 4 chi-squared test). The difference, a decreasing number of juveniles from September through May can be seen in Figures 6-1 and 6-3. In addition to egg production, there are, of course, a multitude of factors governing the number of juveniles in a population, e.g. egg survivorship, hatchling survivorship. In addition, sampling bias (Juveniles are harder to see and catch than large lizards.) or juvenile behavior may vary from period to period.

The paired abdominal fat bodies of female *A. humilis* are largest in September and small in all other months (Fig. 6-1). There is no apparent correlation between fat body size and gravidity. Given the lack of reproductive variability, this is not surprising.

Males.

Like the females, male *A. humilis* seem to be relatively acyclical. Testis weight fluctuates only slightly from season to season. The difference between the highest mean testis weight (February) to the lowest (November) is only 26% of the highest (Fig. 6-4). In contrast, Caribbean anoles may have testis weight declines of more than 80% (*A. grahami* on Bermuda) and usually have 60-70% declines where a notable seasonal testis regression occurs (Licht and Gorman, 1970). Where Licht and Gorman found no evidence of testicular cycling, (*A. richardi* on St. Vincent), there is still a maximum difference of over 35% of the highest mean testis weight. Compared to these, the differences found in *A. humilis* are minor.

Fat bodies of males average smaller than those of the females, and they are smallest in May (Fig. 6-4). Maximum mean fat body weight is only 2.7 times the minimum. In contrast, fat bodies in a seasonal Costa Rican anole, *A. cupreus*, may increase during non-reproductive period to 10 or 15 times their wet season weights (Fleming and Hooker, 1975).

4. Results for *Anolis limifrons*

Anolis limifrons is slightly larger than *A. humilis*, so the minimum size of reproductive animals is also larger. The smallest class II female was 34 mm SVL, thus only those 35 mm or longer were used. Testis weight in 150 males is correlated to SVL ($r=0.83$, $P<.01$); least squares linear regression gives a slope of 1.21 mg/mm. To minimize the effect of body size on testis size, no males less than 33.5 mm SVL were used.

Females.

The reproductive pattern of *A. limifrons* females is quite similar to that of female *A. humilis*. All are reproductive in all periods except February, and gravidity decreases in both February and September (Fig. 6-5). In this species, however, one shift in proportion gravid in adjacent periods is significant, 76% gravid in February versus 97% in May ($P<.05$, 2 x 2 chi-squared test). When proportion of gravid females with two ovidcual eggs are compared for adjacent periods, differences are not significant.

Rainfall does seem to affect egg production in *A. limifrons*. When September and February (dry seasons) are combined and compared to November and May (wet seasons) combined, the dry season has a significantly lower proportion gravid ($P<.01$) and rate of egg production ($P<.05$). This is unlike Río Frío *A. humilis* which did not have a significant dry season decline in either measure of reproductivity.

Temperature is apparently not as important as rainfall. There is no significant difference in gravidity or rate of egg production between a combined cool (November and February) sample and a combined warm (September and May) sample (Table 6-4).

Slight declines in the proportion of juveniles in the November and May samples are probably reflections of the declines in gravidity and egg production rate during September and February (Fig. 6-5, 6-6). They may also be due to reduced hatching or juvenile survival during the drier periods. The differences are not significant ($P>.05$, 2 x 4 chi-squared test).

Fat bodies are largest in *A. limifrons* females in periods when egg production (percent gravid) is low (Fig. 6-5). This is as expected from the similar finding of Licht and Gorman (1970) and Fleming and Hooker (1975). For *A. limifrons* females, the magnitude of difference between periods is not great, the heaviest mean being only 3.1 times the lowest mean.

Males.

As in *A. humilis*, testis weight in *A, limifrons* shows no clear relationship to either rainfall or temperature (Fig. 6-7). There does, however, appear to be a correlation between mean testis weight and day length. Testis weights are lowest in November when photoperiod is minimal and highest in May where day length is longest. This pattern is as one might expect from the experimental data of Licht (1966, 1967a, b, 1969a, b, 1971) and Fox and Dessauer (1958) for *A. carolinensis*, but the amount of difference is not nearly as great as can occur in other anoles. In Río Frío *A. limifrons*, the lowest mean testis weight is only 19.4% less than the highest. Male anoles with strong seasonal testicular regression often have lowest mean testis weights of only 5-25% of the mean weight in periods of greatest testicular activity (Licht and Gorman, 1970; Fleming and Hooker, 1975).

Fat body weight is very low with only slight variation, yet it is almost inversely related to testis weight (Fig. 6-7). The only exception is the September mean which is slightly higher than the November mean instead of slightly lower.

5. Results for Other *Anolis*

Samples of the other six species of *Anolis* were not adequate to define fully the reproductive cycles. Only in male *A. lemurinus* were appropriate, though small, samples available from all four periods. As a result, only partial comparisons can be made.

Anolis carpenteri.

Only a few adult female *A. carpenteri* were collected with none taken in either November or May, the two "wet" periods. All eight specimens were reproductive in the September sample, with six of those gravid. All three in the February sample were gravid (Fig. 6-8). A 2 x 2 chi-squared test indicates that the proportion gravid in these small samples is not significantly different (Table 6-4). In each gravid female, only one oviducal egg was present. Measurable fat bodies were not present in any of the February females and in few of the September specimens (Fig. 6-8). Since these are the periods (dry season and *veranillo*) when reproduction should be low and fat storage high if seasonality occurs, *A. carpenteri* females probably produce eggs throughout the year.

Very few juveniles were collected (Fig. 6-9) at Río Frío. Two small males in the November sample probably hatched during the *veranillo*. Fitch (1975) also found only a few small individuals. Two 32 SVL specimens from Finca La Selva he attributed to July and October breeding, and two small (28 and

32 mm SVL) specimens from Turrialba he attributed to October or November breeding.

Male *A. carpenteri* were not collected in May, and November and February samples are small. Testis weights are very low in *A. carpenteri* in all samples (Fig. 6-10). This may be just an artifact of the extremely slim, habitus of the species (See section IV), but male *A. limifrons* of similar length weigh only about 30% more (Table 4-1), yet have testis weights approximately five times as great. Sperm were abundant in most September males, but in both November and February, sperm were few and epididymises were not greatly swollen. This would suggest a reduction in testicular activity from at least September through February, but with no May samples this can not be verified. Fat bodies are small in September and not found in any November or February males.

Anolis lemurinus.

Inadequate samples of female *A. lemurinus* were collected in November and February. All in the September and May samples were gravid, with four of six in each having two oviducal eggs (Fig. 6-11). The only November specimen, a large female, was non-reproductive, though from the size of the oviducts and the large corpora lutea, it is apparent that she had been reproductive in the recent past. In the February samples only two females were of adult size; one was gravid and the other was non-reproductive. Ovidcuts were small and corpora lutea lacking in the class I female, indicating that she had probably just reached reproductive size during the dry season, but had not yet produced eggs. Possibly because of the small samples, wet vs. dry and warm vs. cool comparisons are not significant. Fat bodies are small during September and May (Fig. 6-8), but the sample sizes preclude meaningful comparisons with November and February females.

The proportion of juveniles in the samples also seems to indicate a November-February decline in reproductivity (Fig. 6-11), 6-12). Few juveniles were found in February and none in May. At Finca La Selva, however, Fitch (1975) found a gravid female in December and a hatchling in February, probably from a December egg. Nine young from 39 to 47 mm that Fitch found from February to May he attributed to egg-laying from October to January. This would seem to indicate that the decline in female reproduction is probably limited to the January--March dry season.

Small but adequate samples of male *A. lemurinus* were collected in all four periods, with an additional four individuals collected during the preceding August, just at the start of the *veranillo*. Figure 6-13 shows the clear pattern of testis regression as day length decreases through November. Testes enlarge in November and May, increasing day length, to slightly larger than the August mean. Fat body size increases from August through February and drops off sharply in May. The fattening seems definitely related to testis weight, but lagging slightly behind. There is no apparent correlation between either rainfall or temperature and either fat body or testis size.

Anolis pentaprion.

Only six adult female *A. pentaprion* were collected, two each in September and November, and one each February and May. All six were reproductive; all were gravid except one of the two November specimens. That non-gravid female had enlarged oviducts and had probably recently deposited an egg, one follicle was enlarged and yolky. All had small (>5.5 mg) fat bodies, except the single non-gravid female. Her fat bodies weighed 29 mg. Egg production apparently continues through the dry season, but possibly with some seasonal decline.

The only juvenile *A. pentaprion* found were in the September sample (Fig. 6-14), indicating July-early August egg-laying. Smith and Kerster (1955) found a number of eggs of this species in bromeliads in Chiapas, Mexico, during July and early August. As Fitch (1975) suggested, the high-arboreal habitat of *A. pentaprion* may expose it and its eggs more directly to the effects of reduced rainfall.

Male *A. pentaprion* were also not collected in adequate numbers, four each in September and November, one in February and none in May. Testis weights declined from a mean of 12 mg in September to a mean of 8.8 mg in November. The single February male had much heavier testes, 29 mg, suggesting the familiar September-November regression and a February increase (Fig. 6-15). Fat body sizes are high in September and decrease in November and February, but differences are not significant.

Anolis lionotus.

Adequate samples of the riparian *A. lionotus* were not taken during the first two collecting periods. Only a single male, and no females, was collected in each of September and November. All large females were reproductive in both February and May, all but one in each were gravid. Fat bodies were small in females in both periods. There are no significant differences in gravidity, rate of egg production (Table 6-4) or fat body weight. An annual cycle can not be characterized, but it is apparent that egg production is high during the dry season, so probably continues all year. Juveniles were found in all samples except May (Fig. 6-16). As Fitch (1975) reported young from all parts of the year, the lack of young in my May sample is probably an anomaly.

It is likely that male *A. lionotus* are also reproductive all year. Testis weights were lowest in the two individuals from September and November and highest in the May sample. Sperm were abundant in the September specimen, few in the November specimen and abundant in February and May males. A moderate testis size reduction may occur during the short days, but tests are far from minimal (Fig. 6-17). Fat bodies are small in all but a few May males, which cause an obvious but non-significant difference (Fig. 6-17).

Anolis capito.

Only five female *A. capito* of reproductive size were collected, two each in September and February, and one in

November. All were gravid and had small (<6 mg) fat bodies except for one September individual, which was a non-gravid reproductive with moderately large (52 mg) fat bodies. That individual was also the smallest reproductive female and was probably just entering the reproductive size class.

Young of *A. capito* were found in all three samples (Fig. 6-18). These represent egg-laying in July, August, October, November, December and January. In his Finca La Selva series, Fitch (1975) found young representing egg-laying in every month.

Male *A. capito* were not collected in May, and only two were collected in November. Testis weight is less in the two November individuals than in September or February (Fig. 6-19) indicating a possible short day decline in male reproductivity. Fat bodies were quite variable showing no significant differences among the three periods (Fig. 6-19).

Anolis biporcatus.

The largest anole at Rio Frio, *A. biporcatus* was not collected in May, and only three of reproductive size were taken in February, once again precluding adequate description of reproductive cycles. Two females were collected in August, and neither was reproductive. Both were relatively small, had large fat bodies and no evidence of prior egg production (corpores lutea or enlarged oviducts). In the September sample, 90% were reproductive, but only 50% gravid (Fig. 6-20). In November all were reproductive and 80% gravid. Both February specimens were reproductive.

The distribution of juveniles also suggests a *veranillo* decline in egg production (Fig. 6-21). One 51 mm SVL juvenile was collected in August; three with a SVL of 55 mm in September and none in November. These would probably all have been hatched during the prior rainy season (May-July). The next evidence of reproduction is a 36 mm SVL hatchling from February, which undoubtedly hatched from an egg produced after the *veranillo*. However, McCoy (1975) found gravid females in Guatemala from August through December. This and records of dry season egg-laying by this species in Mexico (Henderson, 1972) and Guatemala (Fitch, 1975) indicates possible year-round reproductivity in some localities.

Fattening of female *A. biporcatus* is also apparent during the *veranillo* reproductivity decline (Fig. 6-20). Fat body weights are very high in August and September, declining in November, apparently in response to increased reproductive activity.

Male *A. biporcatus* may also have a *veranillo* reproductive decline, as the single August testis weight is low (Fig. 6-22), but the September mean is about the same as the November. February and May samples were not collected. Fat bodies in males are smaller than in females, but the samples are inadequate for inference about cycling.

6. Female Reproductive Cycles

In Costa Rican *Anolis*, the dominant environmental factor influencing egg development is rainfall. In areas where little rain falls during some months of the year female reproduction is greatly reduced. Fleming and Hooker (1975) found no gravid females in 52 *A. cupreus* obtained in Guanacaste Province, Costa Rica, during the December through April dry season. Fitch (1973b) found almost no dry season reproduction in female *A. cupreus* from four localities in Guanacaste or in *A. intermedius* from San José. In these areas rainfall is usually less than 50 mm per month for at least three months of the year.

At Río Frío it is never that dry; minimum mean monthly precipitation (February) is more than 150 mm. The average monthly mean for the four driest months is over 200 mm. Here female anoles show only moderate seasonal variation in reproductive activity. In the two small species with the most reliable samples, *A. humilis* and *A. limifrons*, at least 69% of the mature females are gravid in all seasons. Low gravidity occurs for both species in the *veranillo* and the dry season. Egg production is highest for both in May, the beginning of the wet season. The lowest percent gravidity in any sample of more than three individuals is the September or *veranillo*, sample of *A. biporcatus* in which only 50% are gravid. In an area with a similar rainfall pattern, southwestern Costa Rica, Andrews (1971a) found 78% of female *A. polylepis* gravid in the dry season and 90% gravid in the wet season.

In Panama, at least one species has populations at both extremes. Sexton et al (1971) studied *A. limifrons*[1] in three areas there. Rainfall patterns in their three areas were similar, a January through April dry season and an evenly wet May to December. The major difference in the areas is the severity of the dry season, reflected in the mean annual precipitation - 1.8 m on the Pacific, 2.7 m at mid-isthmus and 3.1 m on the Caribbean side. Río Frío is wetter than any of their sites, 4.3 m per year, and has the *veranillo*. Dry season gravidity in their Caribbean side samples was 44%, 78% at mid-isthmus, and only 6% on the dry Pacific side. During the wet season, all three populations have much greater reproductivity, 93%, 95% and 100% gravid respectively.

Additionally there is some evidence that more exposed species are more affected by rainfall reduction. Two species at Río Frío which inhabit the exposed tree crowns or trunks most of the time, *A. pentaprion* and *A. biporcatus*, show some evidence of reduced reproduction in at least part of the year. Similarly, Sexton et al (1971) found female *A. auratus*, a grassland anole, to be more severely affected by the dry season than the forest dwelling *A. limifrons* from the same general area. At mid-isthmus only 11% of female *A. auratus* were gravid during the dry season, compared to 78% of female *A. limifrons*.

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[1] As noted by Fitch (1973b) Panamanian anoles called *A. limifrons* may be quite different from Costa Rican populations referred to the same species. The Panamanian *A. limifrons*, in at least some localities, are longer, stockier and have a bright orange dewlap. This may represent a difference in species, or just geographic variation.

The suggestion of Gorman and Licht (1974) that temperature, not rainfall determined reproductive activity in female anoles seems to be inapplicable at Río Frío. Specifically, they suggested from their study of Caribbean anoles, particularly lowland and upland populations on Puerto Rico, that ovarian activity falls when average air temperatures drop below some threshhold. In upland populations air temperatures were always lower than in the lowlands, thus seasonal ovarian declines were greater. At Río Frío both mean daily minima and maxima are low from November through March. Yet in all species with adequate samples, more females are gravid in November than in the warmer September. As Figure 6-23 shows, the female reproductive cycle bears much greater resemblance to the rainfall pattern than to the temperature pattern.

Day length has been found to be important in testicular recrudescence in *A. carolinensis* and possibly in ovarian cycling in northern anoles (Licht, 1973). It is probably not an important cue to Río Frío female anoles. The photoperiod pattern almost coincides with the temperature pattern (Figs. 2-2, 2-3, 6-23) so for the reasons stated above, it can be dismissed. In addition, photoperiod is a very symmetrical, one-peak curve. Nothing in this would suggest a mechanism responsible for both a *veranillo* and a dry season overian decrease.

One aspect of the rainfall at Río Frío during the 1970 "dry season" that should be considered is the extraordinary rainfall during February. Normally the driest month of the year, February (519 mm) was the wettest month between November 1969 (747 mm) and December 1970 (1190 mm). Rainfall in April (461 mm) was also above normal. It might seem reasonable that female anoles should have had a February "burst" of gravidity, if, in fact, rainfall is the primary cue for ovarian activity.

It is possible that February samples do contain more gravid females than one would find in a "normal" year. Percent gravidity is actually slightly higher in February than in September for both *A. humilis* and *A. limifrons*. If gravidity were roughly proportional to rainfall[1], you would expect a much greater decline in February than in September during a more typical year.

It is also quite likely that one anomalous storm system would have little overall effect on anole reproduction. Almost 50% of the rainfall received at Río Frío during January through March fell during a two week period. The five weeks preceding and the six weeks following that rainfall were quite normally dry. While rainfall is the obvious environmental factor with which female anole reproduction is correlated, direct intermitantly falling water is probably not the actual cause of the hormonal changes that result in ovulation. It is more likely a combination of soil moisture, relative humidity, cloud cover, wind, temperature fluctuations or any of the other less obvious changes that accompany a "rainy season" or a "dry season." A transient increase in rain might initiate hormonal changes, but with that much rain, most will run off (In fact flooding was extensive during that period.), and very shortly the dry season cues would again be reaching the anoles. Any reproductive hormone increase would then drop back to the more typical levels.

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[1] Sexton et al (1971), in fact, give evidence that ovarian activity in Panamanian *A. limifrons* is not proportional to rainfall, but rather "turned-on" or "turned-off" at some appropriate threshhold.

7. Interspecies Differences in Egg Production Rate

Licht and Gorman (1970) found some evidence that more cyclic species tended to have higher proportions of class IV females, i.e. faster egg production, than did species that had little change in reproductivity through the year. Though all species at Río Frío are relatively acyclic there is some difference in proportion of class IV females (Table 6-7), and these differences are significant ($P<.05$, 2 x 8 chi-squared test).

One hypothesis that would be related to Licht and Gorman's observations is that "annual" species, those that are relatively small and short-lived, must produce their progeny in a relatively short time. These would be expected to have a higher proportion of females in class IV than would the larger, longer-lived species. Using the estimates of Fitch (1973a) the eight species were divided into annual (*A. humilis, A. limifrons* and *A. carpenteri*) and long-lived species (all others), but the difference in proportion in classes III and IV is not significant ($P>.05$, 2 x 2 chi-squared test). This indicated that the annual species produce eggs no faster than larger species.

Another possibility is that relatively slim, scansorial lizards like anoles are burdened by carrying eggs and that carrying two eggs is a significantly greater burden than one egg. As a result it might be expected that more arboreal species would be less likely to carry two eggs, class IV. Comparing the proportion of gravid females in classes III and IV, for three crown-dwelling species, *A. carpenteri, A. pentaprion* and *A. biporcatus*, versus all other shows a significant difference ($P<.01$, 2 x 2 chi-squared test). A similar comparison between the three ground-dwelling species, *A. humilis, A. capito* and *A. lionotus* was not significant. Thus, it would seem that anoles of the crown habitat produce eggs at a slower rate than others, possibly because of increased need for low weight and/or agility.

8. Male Reproductive Cycles

Reproductive activity in male anoles is harder to quantify and explain than is that of the females. Follicle enlargement and oviducal eggs are direct evidence of female reproductivity. In male *Anolis*, however, the evidence is more complex. Testis enlargement is apparently a function of age or size and certain environmental cues, but testis size is not a clear indication of gamete production. Though a "marked decline in testis weight reflects a decline in the rate of spermatogenesis" (Licht and Gorman, 1970), apparently viable sperm are present in small males and large males with either large or small testis. Also, testis size and/or sperm production is not necessarily a measure of reproductive activity. In males, the reproductive activity basic to actual reproduction is courtship and copulation, but territorial defense is apparently also necessary. The intensity of these activities undoubtedly varies considerably with season. Gorman (1967) and Rand (1967b) found copulation and territorial defense throughout the year in *Anolis* in the Lesser Antilles and Jamaica, and Sexton et al (1971) reported copulation by *A. limifrons* during the dry season in Panama. Yet Fleming and Hooker (1975) found a complete absence of such activity in *A. cupreus* during the dry season, and Jenssen (1970) noted a decline of territoriality in Mexican *A. nebulosus* during at least part of the year. No seasonal quantification of these activities is available for any of the Río Frío anoles. In the absence of such, testis size will be used to denote male reproductivity with the understanding that testicular hormones, the levels of which may or may not be directly affected by testis size (Licht and Gorman, 1970), both directly or indirectly influence the amount of sperm produced and delivered to the female.

In all species of Río Frío *Anolis* for which adequate samples are available, there appears to be some seasonal variation in testis weight. Even though the reductions in size are not as pronounced as those occurring in other anoles in more severe environments, the changes represent an obvious and reasonably consistent cycle (Fig. 6-24).

Testis size is lowest in November and maximal by February. High May weights and slightly lower September weights suggest a pattern of increase beginning in January with the maximum reached in February and maintained through mid-year. Decline in testis size probably starts in August or September. This is very similar to, but not nearly as pronounced as, the cycle in male *A. cupreus* from Guanacaste, Costa Rica (Fleming and Hooker, 1975). Similar, but often chronologically different, testicular cycling occurs in many Caribbean anoles (Licht and Gorman, 1970; Ruibal et al., 1972) and in other Central American anoles (Sexton, et al, 1971). Definitely attributing these cyclic fluctuations in testis weight is not presently possible.

It seems relatively clear that rainfall does not provide a direct cause for either testis decline or recrudescence. The low point in testis weight at Río Frío is reached in November or December, usually among the wettest months of the year. Recrudescence begins during the dry season, and testes of most species reach maximal weights at about the middle of the dry season. Weights are high through the rest of the dry season and begin their annual decline during the latter part of the wet season, near the *veranillo*. While it could be argued that the *veranillo* causes the decline at Río Frío, a similar little dry season is not present at other sites where male anoles exhibit equivalent patterns. The statement has been made that the male cycle "anticipates" the rainfall change by about two months, but if so, it does not seem to include the *veranillo* in the pattern at Río Frío. The cycle has only a single depression, not the double depression of the rainfall pattern.

Experimental evidence points to temperature as a major factor influencing testicular recrudescence in *A. carolinensis*, the northern-most anole (Licht, 1966, 1967a, b, 1969a, b, 1971). Licht has shown that short days and low temperatures are involved in the initiation of testicular growth, but that elevated body temperatures (obtained by basking) are most responsible for the rapid testis enlargement occurring just after the lizards emerge from hibernation. However, it is probable that *A. carolinensis* is not an apt model from which to explain testicular cycles of Río Frío anoles.

Unlike *A. carolinensis*, anoles in tropical Costa Rica do not hibernate. Testis weights of Río Frío anoles reach their maximum while air temperatures are still in the lowest part of their annual cycle, not during the time of increasing temperature. Most Río Frío anoles also have a different thermal preferenda from *A. carolinensis*. With the possible exception of *A. pentaprion*, Río Frío anoles do not raise their body temperatures much above ambient by basking. The trunk-dwelling species, *A. biporcatus*, *A. lemurinus* and *A. limifrons*, might occasionally bask in filtered sunlight to obtain a body temperature one or two degrees above ambient (Fitch, 1973b), but *A. capito, A. humilis, A. carpenteri* and *A. lionotus* rarely, if ever, linger in direct sunlight and so maintain body temperatures virtually the same as the air-substrate temperature (Campbell, 1971, 1973; Fitch, 1973b). The only exception is *A. pentaprion* which apparently basks in the tree crown (Campbell, 1971). Thus in most Río Frío *Anolis*, it is doubtful that an increase in temperature leads to testicular growth.

Photoperiod is a very likely cause of testicular cycling. Testes shrink as daylength begins to decrease, perhaps as soon as it falls below a certain point. Enlargement commences soon after daylength begins to increase. Arguing against daylength is the fact that Licht (1967b) found photoperiod to be only a permissive factor, not a causitive factor. Of course in these species in a tropical climate, photoperiod could be more important. Firm acceptance of such a conclusion would require convincing experimental evidence which is not now available.

Licht (1967b) has also suggested that an "endogenous trigger" may spontaneously affect testicular cycling. He suggests that once this trigger is set, the temperature and daylength govern the cycle. Again experimental evidence is lacking for any such mechanism in tropical anoles.

After all the possible causes are considered, it is reasonable to reconsider the function of testis enlargement. The selective force behind the evolution of any kind of testicular cycling must involve some advantage in inseminating reproductive females. This brings the question back to the rainfall cycle. If the female cycle is governed by rainfall, shouldn't the male cycle be also? Ideally a male should be ready to initiate courtship as soon as females are responsive. In most anoles this means obtaining, defending and holding a territory. This activity is governed by increased testicular hormone levels, and would thus require testis enlargement prior to the onset of female reproductivity. After the egg-laying season is well under way and females have been inseminated, males can conserve resources and fatten up for the next cycle by reducing testis size and the accompanying reproductive activities. At Río Frío this occurs at or just prior to the *veranillo*, even though females will still be reproductive during the late rainy season. In severely seasonal areas, e.g. Guanacaste, such a mechanism might totally stop testicular activity. In the relatively constant climate at Río Frío the male cycle is merely a slight reduction from the high, with some reproductive activity in all seasons.

There is also the somewhat disconcerting fact that male cycles may be totally irrelevant to production of young. Fox (1963) found sperm storage structures in female *A. carolinensis* that are apparently capable of keeping viable sperm for several months. If this occurs in other species, females may only require an occasional insemination to produce fertile eggs at any time. In fact, Fitch (1973a) has shown that small anoles such as *A. humilis* and *A. limifrons* rarely live longer than one year. It is possible that a single copulation could allow a small female anole to produce fertile eggs for life.

9. Fat Cycles and Reproduction

In anoles where reproduction varies greatly through the year, there is usually marked fattening during the non-reproductive periods (Licht and Gorman, 1970; Sexton et al, 1971; Gorman and Licht, 1974, Fleming and Hooker, 1975). At Río Frío both males and females of most species have relatively small fat bodies and relatively high reproduction throughout the year. In some (*A. limifrons, A. carpenteri* females, *A. lemurinus,* and *A. biporcatus* females) the noticable reproductive cycles are mirrored by the fat cycles, but in others there is not a discernable pattern. This general lack of significant fattening is probably due to the relatively high amount of energy expended for reproductive activities throughout the year.

The largest anole at Río Frío has the largest fat bodies. Even adjusted for body size, the fat bodies of *A. biporcatus* are larger than in any of the smaller species. This could be a reflection of a greater decline in reproductive activity, but it is more likely just a result of large body size. Licht and Gorman (1970) reasoned that the giant *A. richardi* expends less of its energy budget for reproductive activities, and thus can store some excess as fat during most of the year. The same may be true of *A. biporcatus*, but larger numbers need to be examined during other parts of the year.

TABLE 6-1.
Usual Trends in Daylength, Temperature
And Rainfall at Río Frio, Costa Rica

PERIOD	SEPTEMBER	NOVEMBER	FEBRUARY	MAY
Daylength	Decreasing	Almost Minimal	Increasing	Almost Maximal
Temperature	High, Decreasing	Low	Low	High, Increasing
Rainfall	Moderately low	High	Quite Low	High

NOTE: In 1970 rainfall was abnormally high during February and abnormally low during May.

TABLE 6-2.
Length of Females in Reproduction Samples

	humilis	*limifrons*	*carpenteri*	*lemurinus*
SEP	35.29±0.47(19)[†]	38.52±0.35(32)	39.94±0.84(8)	56.83±1.10(6)
NOV	35.92±0.53(12)	37.35±0.41(10)	41.17±0.67(3)	57.5 (1)
FEB	34.45±0.36(20)	38.32±0.29(34)		55.50±2.00(2)
MAY	34.53±0.40(16)	39.25±0.34(32)		55.83±1.19(6)
	pentaprion	*lionotus*	*capito*	*biporcatus*
SEP	57.50±0.50(2)		79.50±2.50(2)	86.95±1.44(10)
NOV	53.75±2.25(2)		87.0 (1)	88.00±1.77(5)
FEB	57.0 (1)	57.23±0.66(13)	82.0 (2)	84.25±0.25(2)
MAY	56.0 (1)	59.17±1.76(3)		

[†] Given as mean ± standard error (sample size).

TABLE 6-3.
Length of Males in Reproduction Samples

	humilis	*limifrons*	*carpenteri*	*lemurinus*
SEP	32.73±0.35(13)[†]	36.24±0.26(27)	35.61±0.46(14)	47.25±0.76(8)
NOV	32.78±0.33(18)	36.24±0.20(19)	35.67±0.17(3)	47.80±1.52(5)
FEB	32.68±0.40(14)	36.34±0.23(22)	35.75±0.75(2)	45.09±0.58(11)
MAY	32.86±0.24(22)	36.73±0.26(41)		45.10±1.05(5)
	pentaprion	*lionotus*	*capito*	*biporcatus*
SEP	57.25±2.28(4)	57.0 (1)	73.10±0.58(5)	87.23±0.61(16)
NOV	53.88±1.85(4)	57.5 (1)	65.25±2.25(2)	86.10±1.03(5)
FEB	66.5 (1)	61.71±3.46(12)	72.63±4.36(4)	86.0 (1)
MAY		64.14±2.08(7)		

[†] Given as mean ± standard error (sample size).

TABLE 6-4.
Chi-squared Calculated from 2x2 Contingency Tables

TEMPERATURE - COLL(NOV AND FEB) VS. WARM(SEP AND MAY)

	GRAVIDITY		EGG PRODUCTION RATE	
A. humilis	0.032	n.s.[†]	0.376	n.s.
A. limifrons	0.031	n.s.	0.016	n.s.
A. carpenteri	0.006	n.s.	Φ	
A. lemurinus	3.464	n.s.	0.059	n.s.
A. pentaprion			Φ	
A. lionotus[∇]	0.055	n.s.	0.015	n.s.
A. capito				
A. biporcatus	0.147	n.s.	0.000	n.s.

RAINFALL - DRY(SEP AND FEB) VS. WET(NOV AND MAY)

	GRAVIDITY		EGG PRODUCTION RATE	
A. humilis	1.526	n.s.	0.000	n.s.
A. limifrons	8.199	**	4.977	*
A. carpenteri				
A. lemurinus	0.457	n.s.	0.048	n.s.
A. pentaprion			Φ	
A. lionotus[∇]	0.055	n.s.	0.015	n.s.
A. capito				
A. biporcatus	0.374	n.s.	0.045	n.s.

[†] Significance as in Table 4-2.

[Φ] None had 2 oviducal eggs, so no comparison could be made.

[∇] Because only February and May samples are available, there is no difference between rainfall and temperature comparisons.

TABLE 6-5.
Percent Gravid and Fat Body Size in Females

SPECIES	SEP	NOV
humilis	73.7%(1.00±0.29)19[†]	83.3%(0.37±0.12)12
limifrons	68.8%(0.86±0.25)32	90.0%(0.39±0.28)10
carpenteri	75.0%(0.51±0.25)8	
lemurinus	100.0%(5.68±2.27)6	0.0%(25.3) 1
pentaprion	100.0%(1.30±1.30)2	50.5%(15.45±13.45)2
lionotus		
capito	50.0%(26.85±24.95)2	100.0%(12.0) 1
biporcatus	50.5%(217.4±57.7)10	80.0%(98.26±35.99)5

[†] Given as % gravid (mean fat body weight in mg ± standard error sample size.

TABLE 6-5 - extended

FEB	MAY
75.0%(0.43 0.14)20	93.8%(0.50 0.20)16
76.5%(1.19 0.47)34	96.9%(0.70 0.21)32
100.0%(0.00) 3	
50.0%(12.30 7.40)2	100.0%(6.33 1.43)6
100.0%(3.1) 1	100.0%(5.4) 1
92.3%(1.75 0.42)13	66.7%(1.23 1.23)3
100.0%(3.05 3.05)2	
50.0%(8.9 3.80)2	

TABLE 6-6. Testis Weight and Fat Body Size in Males

SPECIES	SEP	NOV	FEB	MAY
humilis	t[†] 10.68±0.78(10)[Φ]	9.24±0.68(17)	12.53±1.16(9)	10.55±0.40(22)
	f 0.90±0.39(13)	0.72±0.17(18)	0.89±0.18(14)	0.41±0.14(22)
limifrons	t 14.91±0.72(23)	12.36±0.72(18)	14.26±1.01(18)	15.33±0.38(41)
	f 0.79±.15(27)	0.69±.17(19)	0.50±.14(22)	0.34±.10(41)
carpenteri	t 2.67±0.13(10)	2.10±0.68(3)	3.10±0.70(2)	
	f 0.31±0.14(14)	0.00 (3)	0.00 (2)	
lemurinus	t 9.27±1.52(3)	4.10±1.14(4)	13.75±1.72(4)	11.82±0.77(5)
	f 3.36±0.70(8)	4.06±0.85(5)	4.44±1.52(11)	1.14±0.69(5)
pentaprion	t 12.05±7.85(2)	8.77±2.71(3)	29.0 (1)	
	f 16.50±6.99(4)	9.78±3.96(4)	7.5 (1)	
lionotus	t 22.8(1)	23.7(1)	27.55±1.63(4)	36.29±4.22(7)
	f 3.7(1)	0.8(1)	2.65±0.51(12)	22.23±10.07(7)
capito	t 51.10±3.14(4)	37.00±0.10(2)	50.15±10.70(4)	
	f 8.26±4.28(5)	3.35±1.55(2)	3.20±1.77(4)	
biporcatus	t 64.81±1.74(11)	66.22±9.62(5)		
	f 97.42±21.50(16)	38.16±23.40(5)	12.4 (1)	

[†] t=testis, f=fat bodies

[Φ] Given as mean weight (mg) standard error (sample size).

TABLE 6-7.
Number of Eggs in Gravid Females

SPECIES	CLASS III	CLASS IV	% CLASS IV
	1 EGG	2 EGGS	
A. humilis	40	14	25.9
A. limifrons	66	22	25.0
A. carpenteri	9	0	0
A. lemurinus	5	8	61.5
A. pentaprion	5	0	0
A. lionotus	10	4	28.6
A. capito	3	1	25.0
A. biporcatus	9	1	10.0

FIGURE 6-1. Seasonality of Reproducitve Activity in Female *Anolis humilis.* Top: Reproduction in Female *Anolis humilis.* Circles with dashed line indicates percent of sample reproductive, i. e. classes II, III, and IV; squares with solid line indicate percent gravid, classes III and IV.

Center: Fat Body Weight in Female *Anolis humilis.* Mean indicated by horizontal line, standard error by stippled bar, 95% confidence interval by vertical line, and sample size by number above figure.

Bottom: Proportion of Juveniles in Samples of *Anolis humilis.*

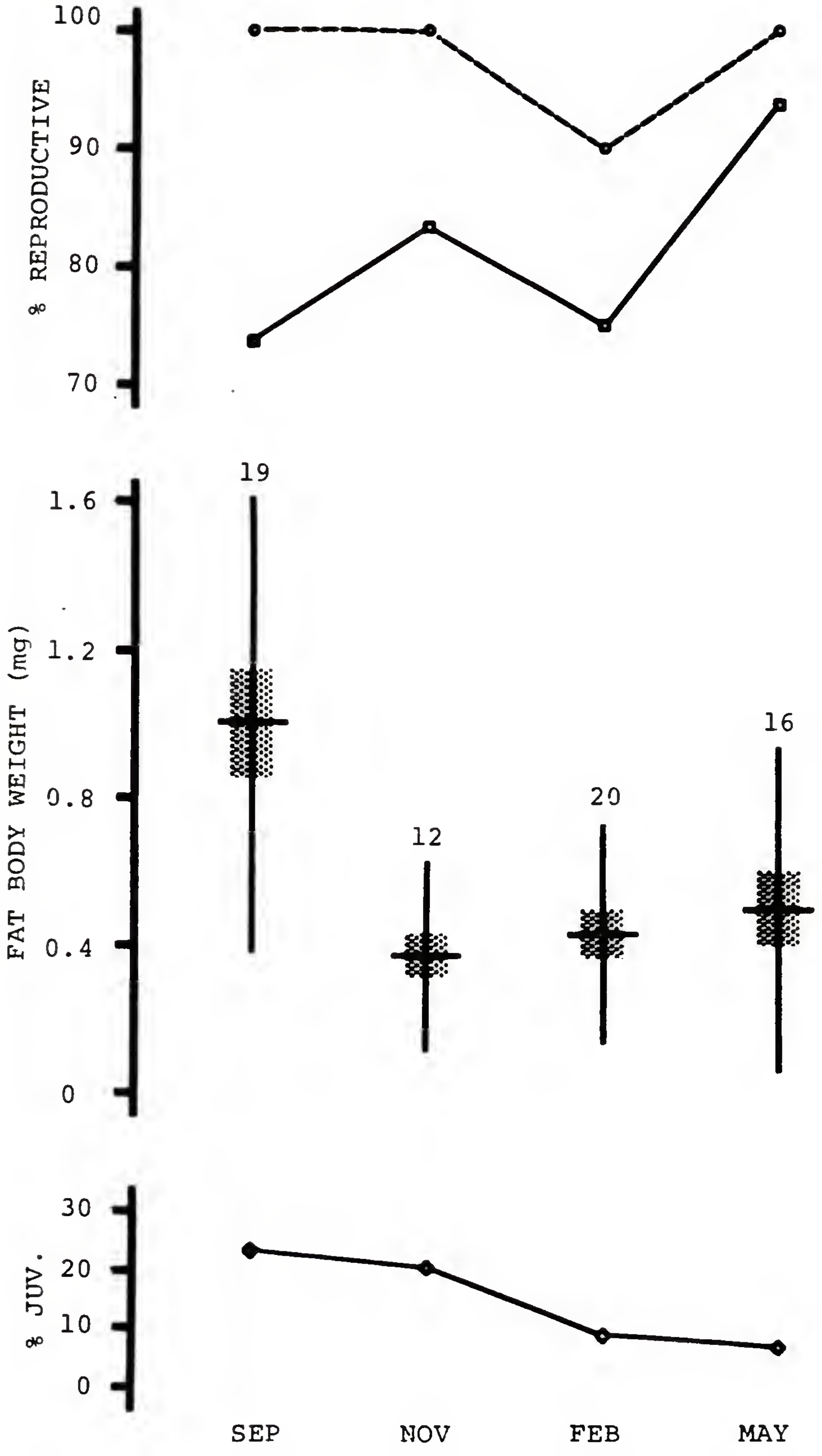

100
90
80
70
% REPRODUCTIVE
1.6
1.2
0.8
0.4
0
FAT BODY WEIGHT (mg)
19
12
20
16
30
20
10
0
% JUV.
SEP
NOV
FEB
MAY

FIGURE 6-2. Relative Frequencies of Females with Two Oviducal Eggs at Different Rates of Egg Production

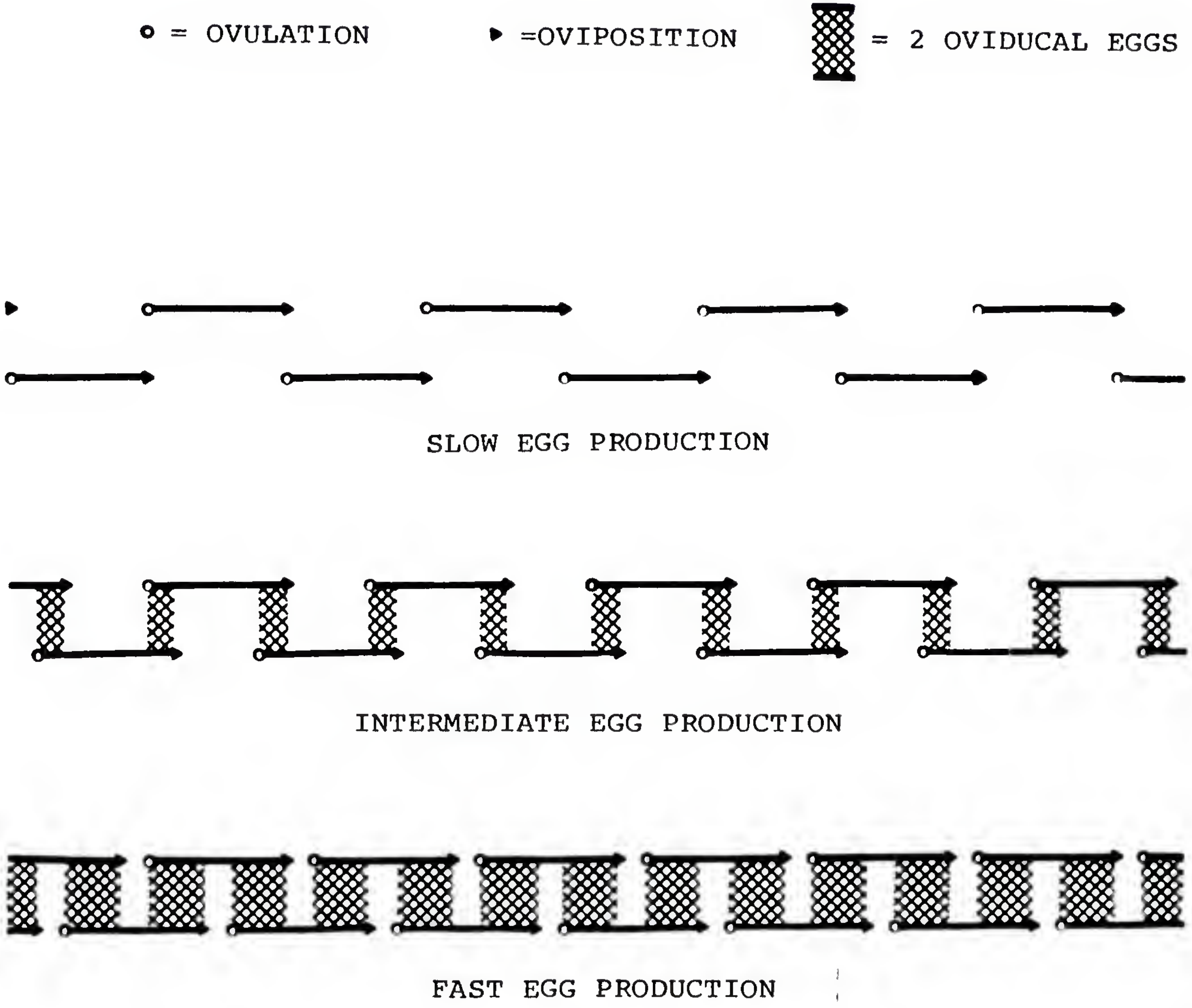

○ = OVULATION
▶ =OVIPOSITION
▨ = 2 OVIDUCAL EGGS
SLOW EGG PRODUCTION
INTERMEDIATE EGG PRODUCTION
FAST EGG PRODUCTION

FIGURE 6-3. Population Structure in *Anolis humilis*. Anoles are grouped in 3 mm size classes. Black bars represent males, striped bars females, and stippled bars unsexed juveniles. Sample size is given below the period designation.

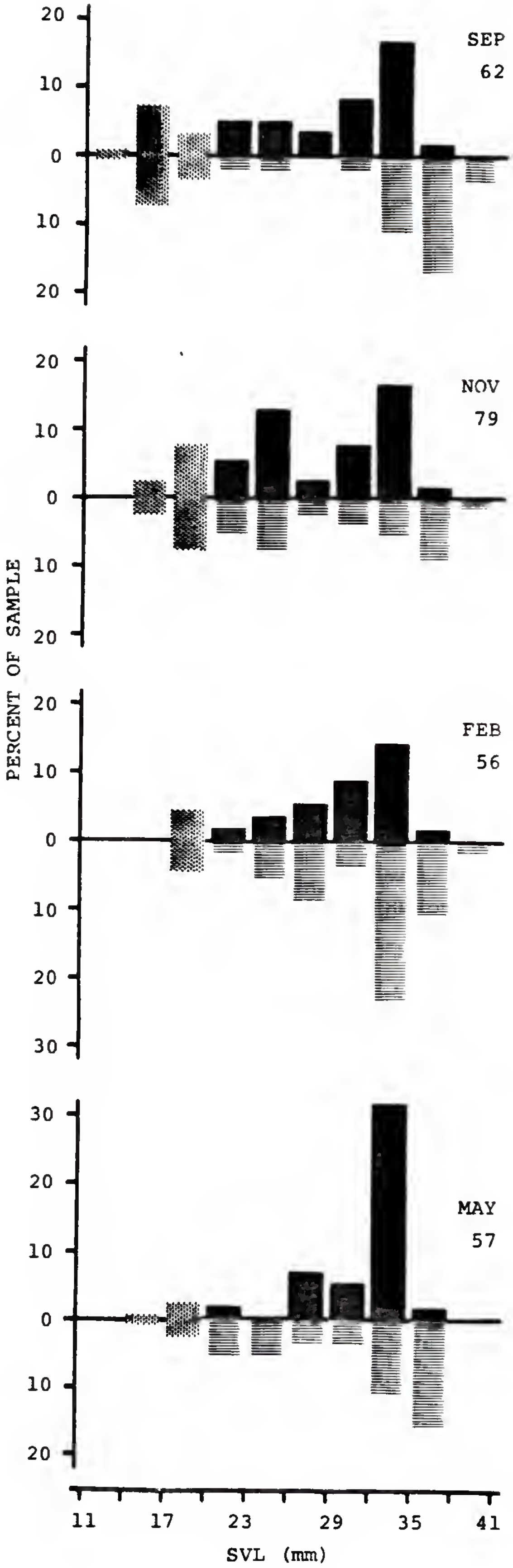

PERCENT OF SAMPLE
20
10
0
10
20
SEP
62
NOV
79
FEB
56
30
MAY
57
11
17
23
29
35
41
SVL (mm)

FIGURE 6-4. Seasonality of Reproductive Activity in Male *Anolis humilis*. Top: Testis Weight in *Anolis humilis*. Mean indicated by horizontal line, standard error by cross hatched bar, 95% confidence interval by vertical line, and sample size by number above figure. Bottom: Fat Body Weight in Male *Anolis humilis*. Mean indicated by horizontal line, standard error by stippled bar, 95% confidence interval by vertical line, and sample size by number above figure.

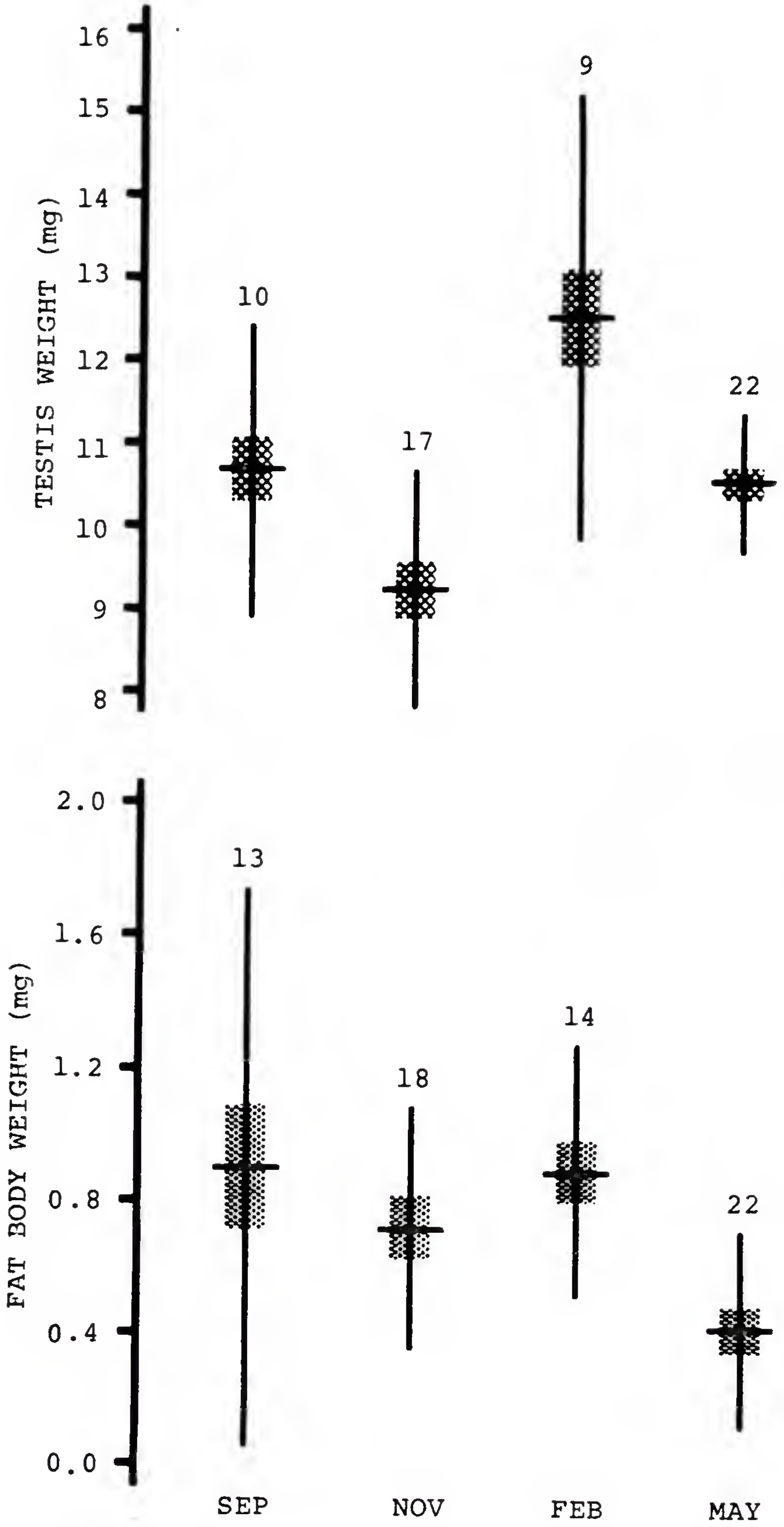

TESTIS WEIGHT (mg)
16
15
14
13
12
11
10
9
8
10
17
9
22
FAT BODY WEIGHT (mg)
2.0
1.6
1.2
0.8
0.4
0.0
13
18
14
22
SEP
NOV
FEB
MAY

FIGURE 6-5. Seasonality of Reproductive Activity in Female *Anolis limifrons*. Lines and symbols are as in figure 6-1.

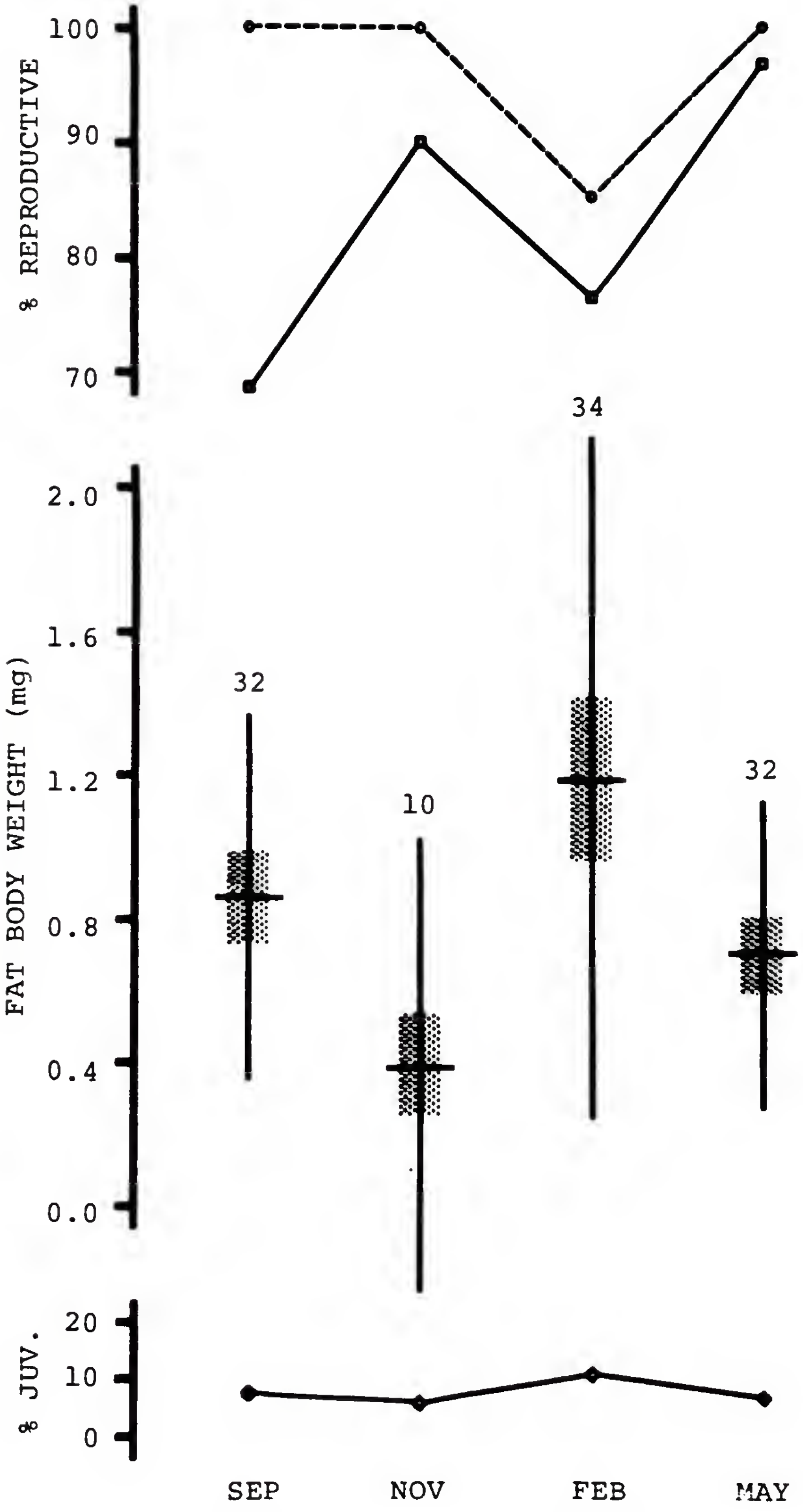

100
90
80
70
% REPRODUCTIVE
2.0
1.6
1.2
0.8
0.4
0.0
FAT BODY WEIGHT (mg)
32
10
34
32
20
10
0
% JUV.
SEP
NOV
FEB
MAY

FIGURE 6-6. Population Structure in *Anolis limifrons*. Arrangement and symbols are as in figure 6-3.

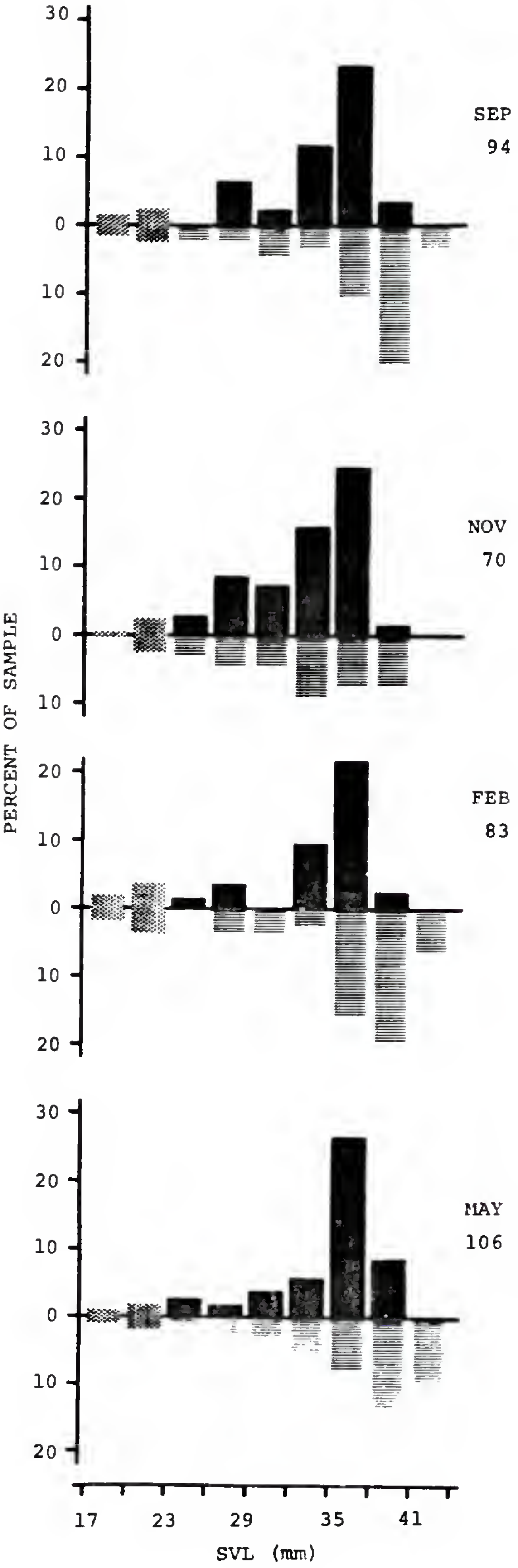

30
20
10
0
10
20
SEP
94
30
20
10
0
10
NOV
70
20
10
0
10
20
FEB
83
30
20
10
0
10
20
MAY
106
PERCENT OF SAMPLE
17
23
29
35
41
SVL (mm)

FIGURE 6-7. Seasonality of Reproductive Activity in Male *Anolis limifrons*. Symbols are as in figure 6-4.

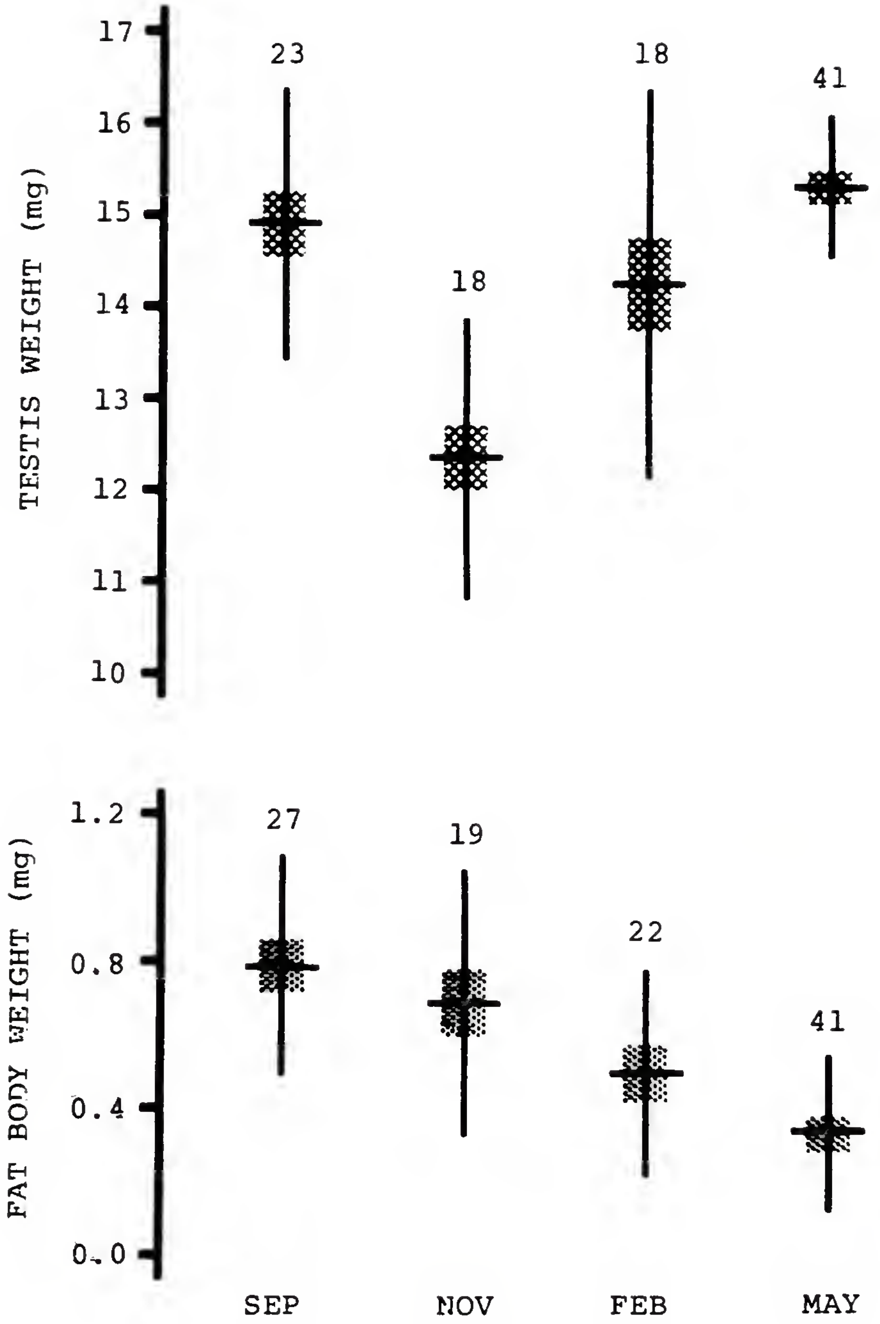

TESTIS WEIGHT (mg)
17
16
15
14
13
12
11
10
23
18
18
41
FAT BODY WEIGHT (mg)
1.2
0.8
0.4
0.0
27
19
22
41
SEP
NOV
FEB
MAY

FIGURE 6-8. Seasonality of Reproductive Activity in Female *Anolis carpenteri*. Top: Reproduction in Female *Anolis carpenteri*. Circles with dashed line indicates percent of sample reproductive, i. e. classes II, III, and IV; squares with solid line indicate percent gravid, classes III and IV.
Bottom: Fat Body Weight in Females *Anolis carpenteri*. Mean indicated by horizontal line, standard error by stippled bar, 95% confidence interval by vertical line, and sample size by number above figure.

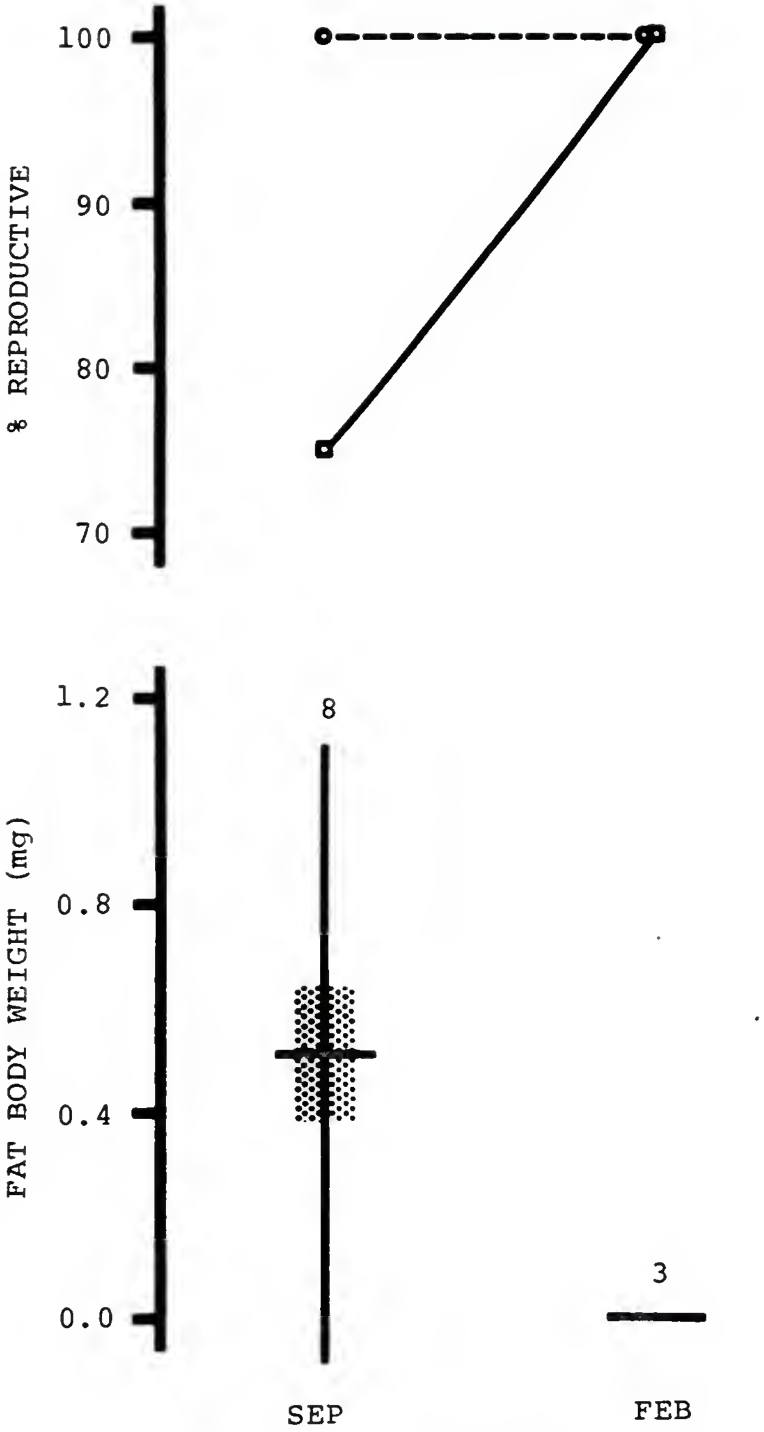

100
90
80
70
% REPRODUCTIVE
1.2
0.8
0.4
0.0
FAT BODY WEIGHT (mg)
8
3
SEP
FEB

FIGURE 6-9. Population Structure in *Anolis carpenteri*. Arrangement and symbols are as in figure 6-3.

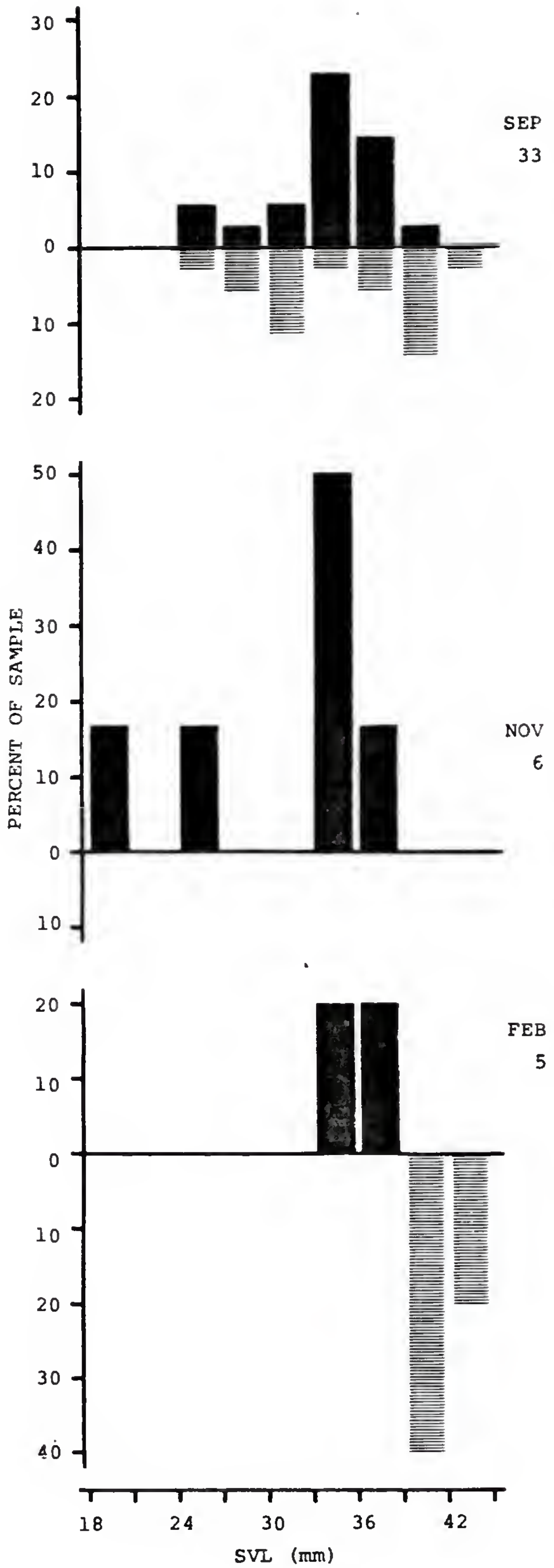

30
20
10
0
10
20
SEP
33
50
40
30
20
10
0
10
NOV
6
PERCENT OF SAMPLE
20
10
0
10
20
30
40
FEB
5
18
24
30
36
42
SVL (mm)

FIGURE 6-10. Seasonality of Reproductive Activity in Male *Anolis carpenteri*. Symbols are as in figure 6-4.

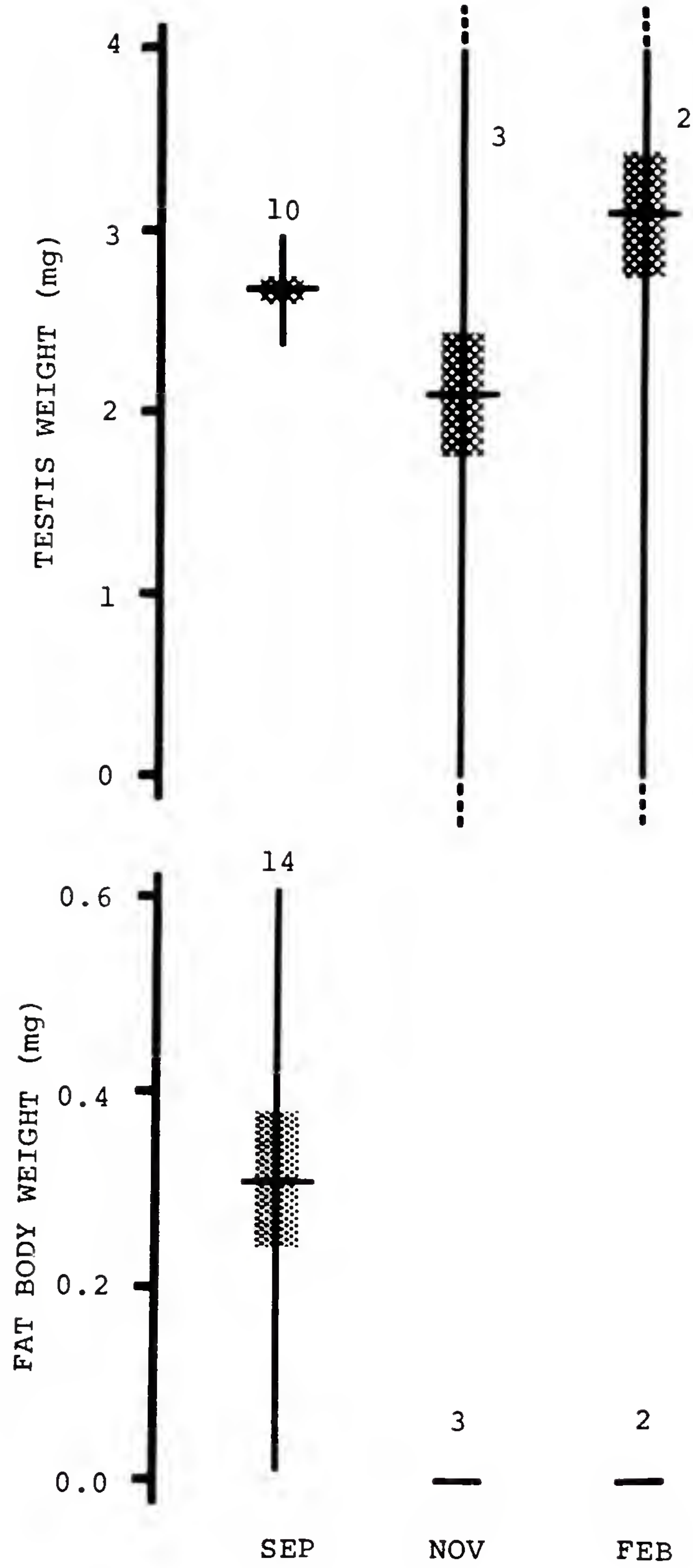
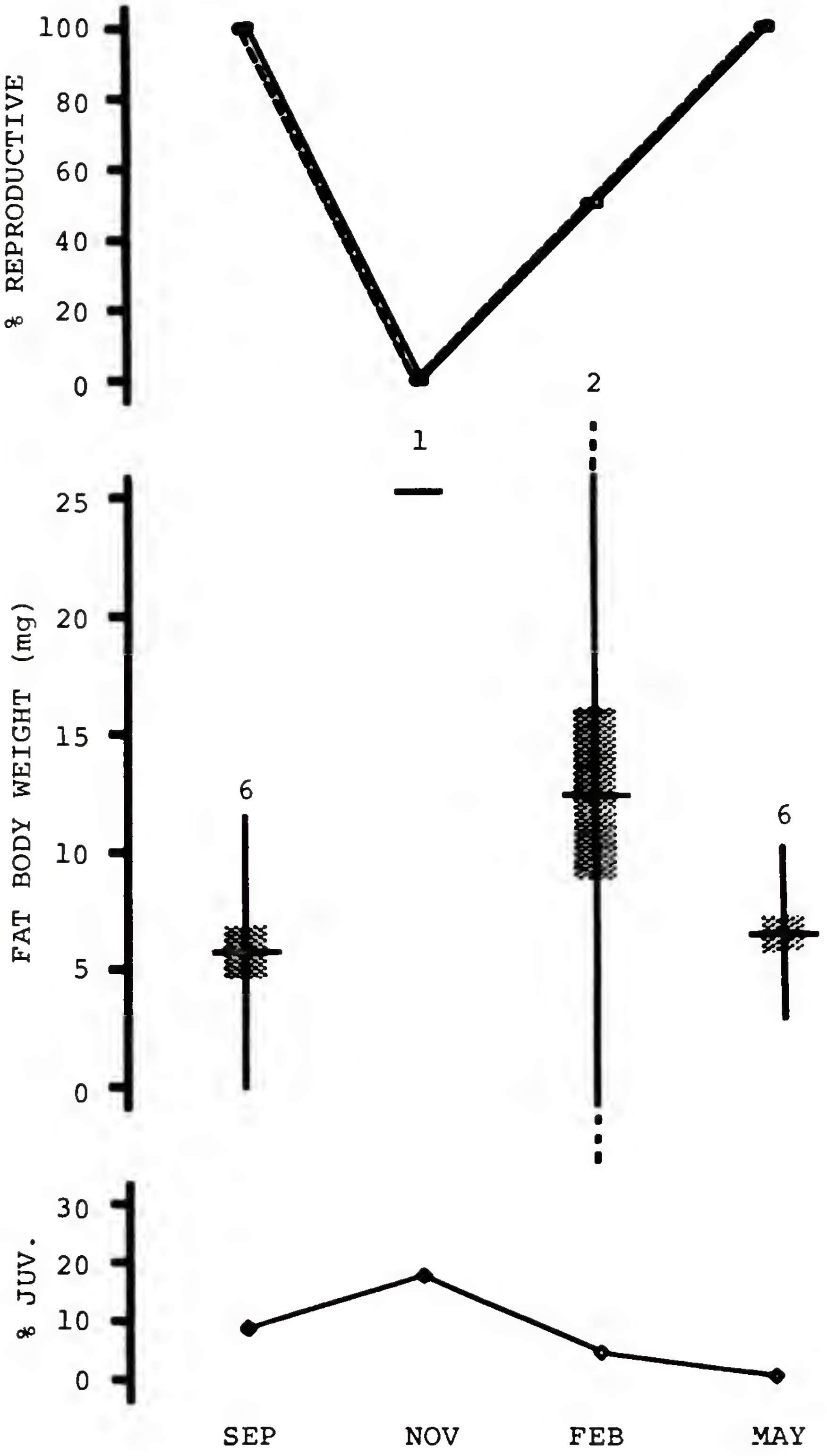

TESTIS WEIGHT (mg)
4
3
2
1
0
10
3
2
FAT BODY WEIGHT (mg)
0.6
0.4
0.2
0.0
14
3
2
SEP
NOV
FEB

FIGURE 6-11. Seasonality of Reproductive Activity in Female *Anolis lemurinus*. Lines and symbols are as in figure 6-1.



% REPRODUCTIVE
100
80
60
40
20
0
FAT BODY WEIGHT (mg)
25
20
15
10
5
0
6
1
2
6
% JUV.
30
20
10
0
SEP
NOV
FEB
MAY

FIGURE 6-12. Population Structure in *Anolis lemurinus*. Anoles are grouped in 4 mm size classes. Symbols are as in figure 6-3.

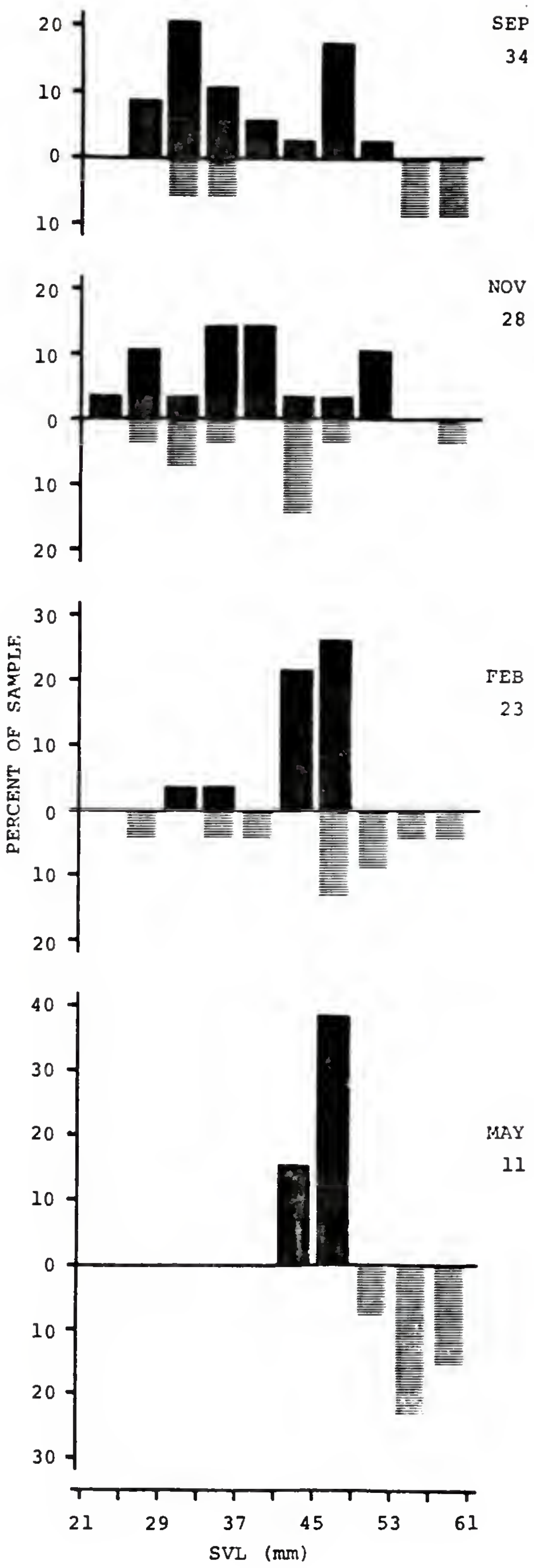

SEP
34
NOV
28
FEB
23
MAY
11
PERCENT OF SAMPLE
20
10
0
10
20
30
40
21
29
37
45
53
61
SVL (mm)

FIGURE 6-13. Seasonality of Reproductive Activity in Male *Anolis lemurinus*. Symbols are as in figure 6-4.

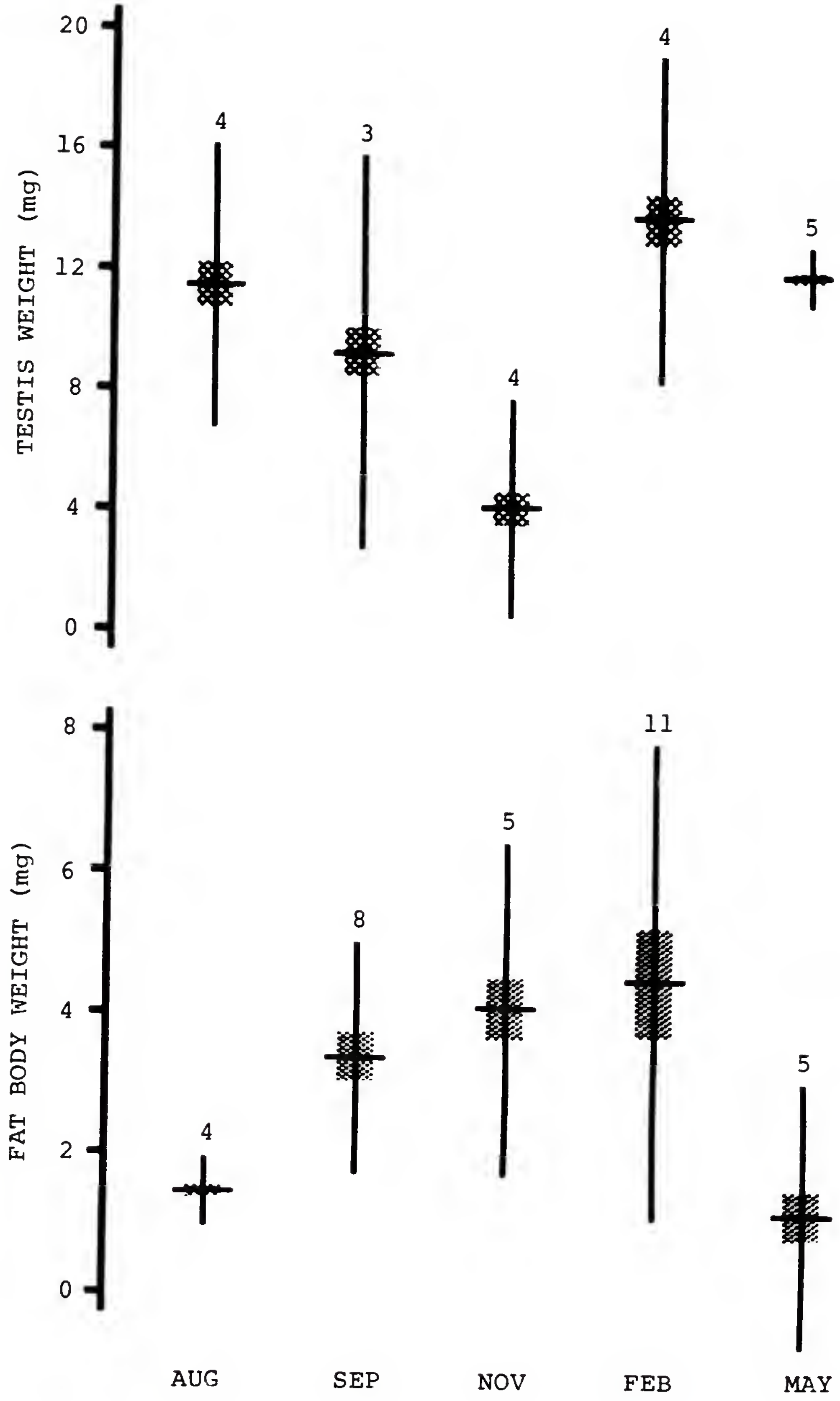

TESTIS WEIGHT (mg)
20
16
12
8
4
0
4
3
4
4
5
FAT BODY WEIGHT (mg)
8
6
4
2
0
4
8
5
11
5
AUG
SEP
NOV
FEB
MAY

FIGURE 6-14. Population Structure in *Anolis pentaprion*. Anoles are grouped in 5 mm size classes. Symbols are as in figure 6-3.

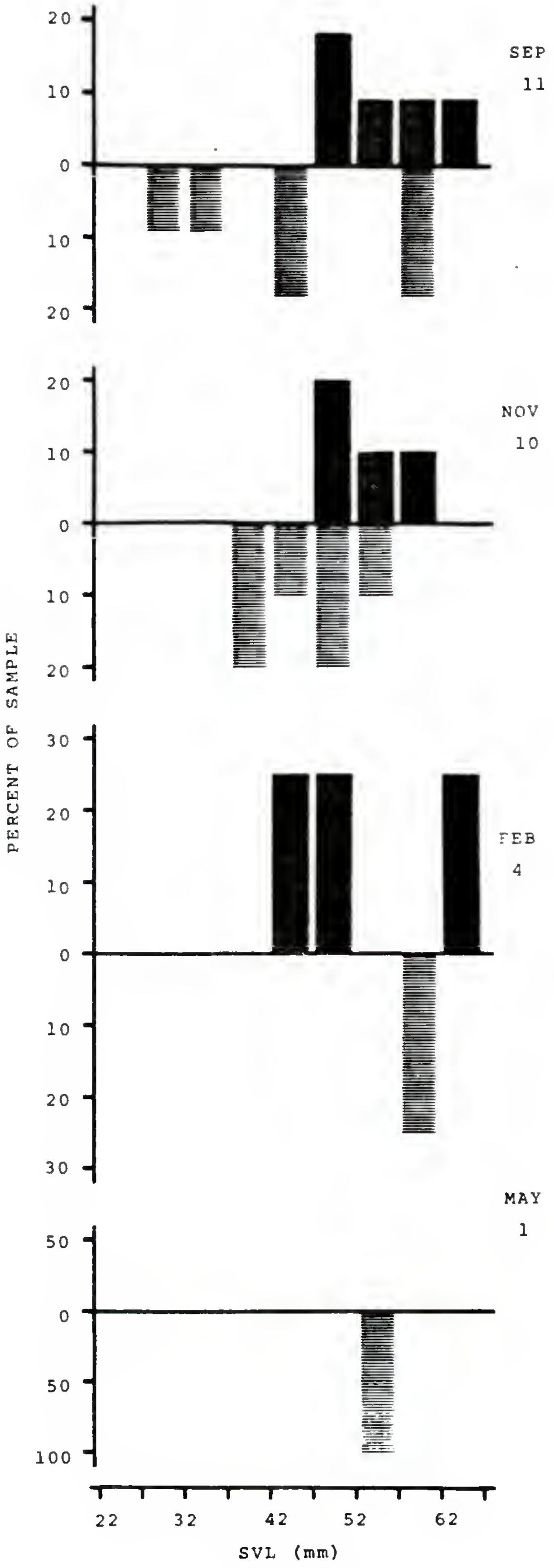

PERCENT OF SAMPLE
20
10
0
10
20
SEP
11
20
10
0
10
20
NOV
10
30
20
10
0
10
20
30
FEB
4
50
0
50
100
MAY
1
22
32
42
52
62
SVL (mm)

FIGURE 6-15. Seasonality of Reproductive Activity in Male *Anolis pentaprion*. Symbols are as in figure 6-4.

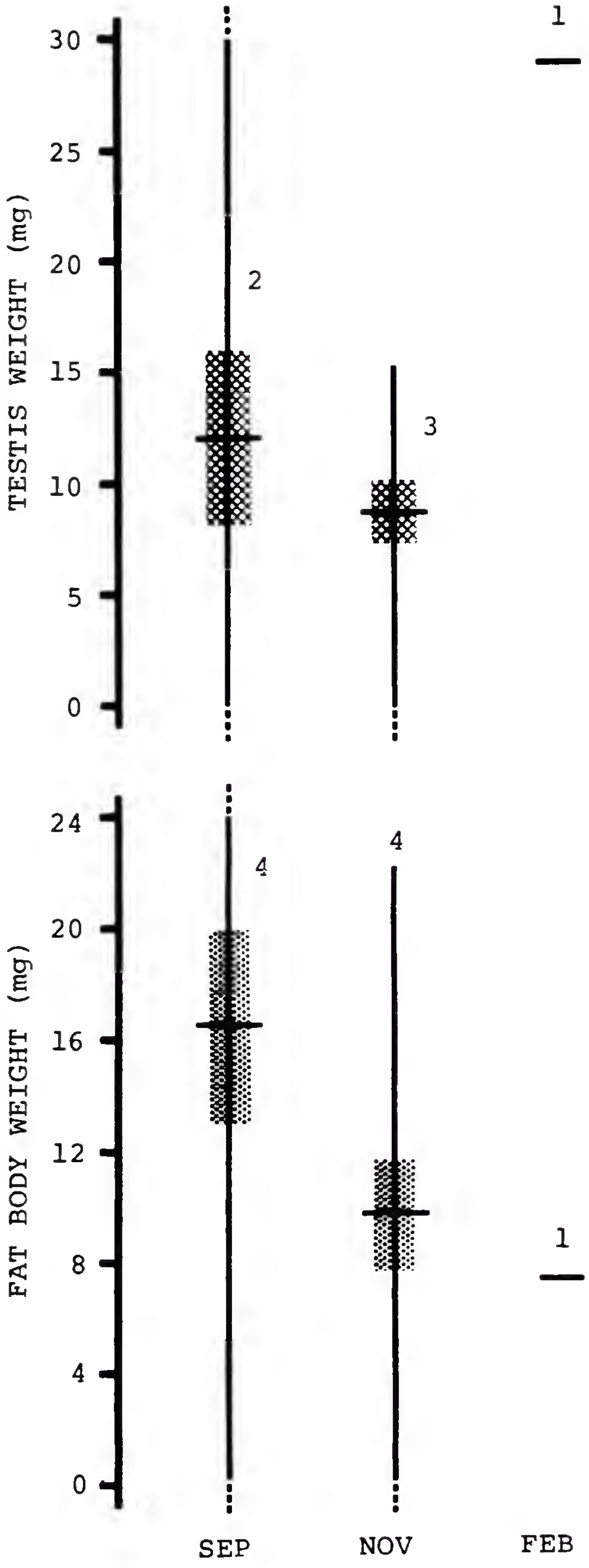

TESTIS WEIGHT (mg)
30
25
20
15
10
5
0
2
3
1
FAT BODY WEIGHT (mg)
24
20
16
12
8
4
0
4
4
1
SEP
NOV
FEB

FIGURE 6-16. Population Structure in *Anolis lionotus*. Anoles are grouped in 6 mm size classes. Symbols are as in figure 6-3.

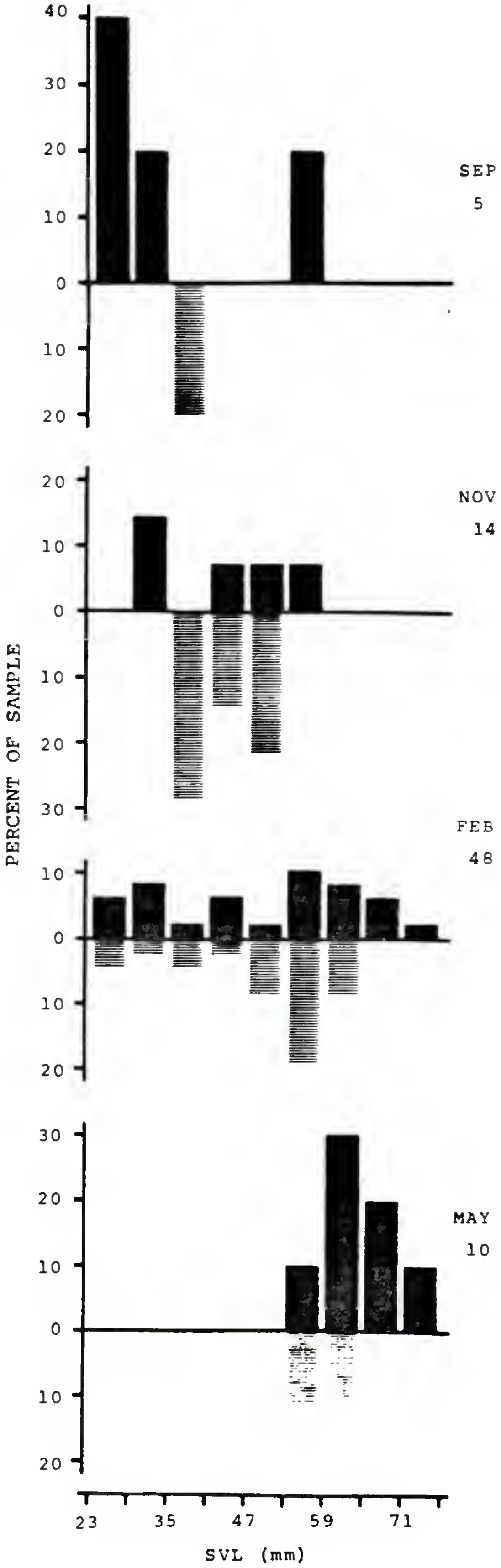

40
30
20
10
0
10
20
SEP
5
20
10
0
10
20
30
NOV
14
FEB
48
10
0
10
20
30
20
10
0
10
20
MAY
10
PERCENT OF SAMPLE
23
35
47
59
71
SVL (mm)

FIGURE 6-17. Seasonality of Reproductive Activity in Male *Anolis lionotus*. Symbols are as in figure 6-4.

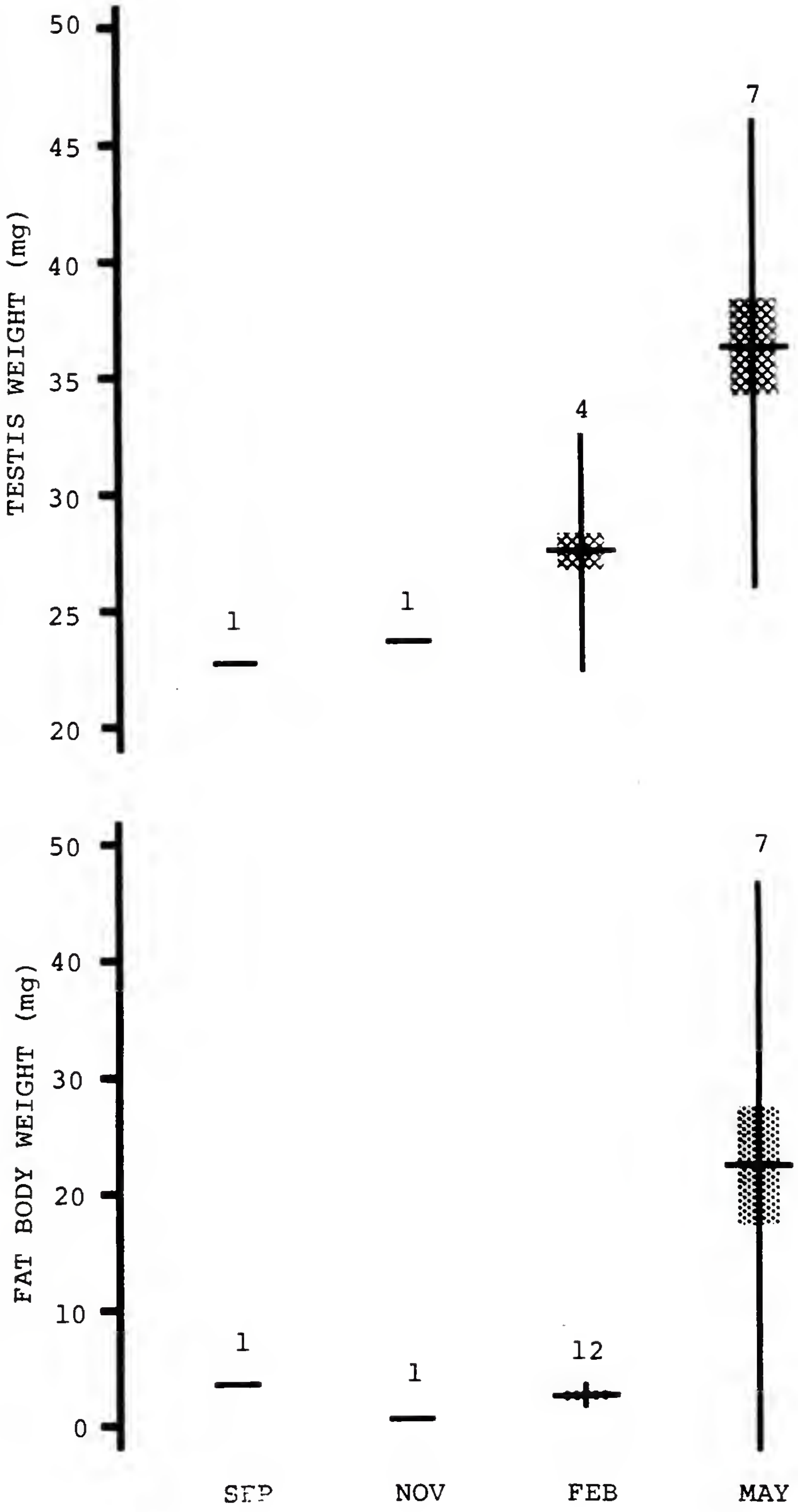

TESTIS WEIGHT (mg)
50
45
40
35
30
25
20
1
1
4
7
FAT BODY WEIGHT (mg)
50
40
30
20
10
0
1
1
12
7
SEP
NOV
FEB
MAY

FIGURE 6-18. Population Structure in *Anolis capito*. Anoles are grouped in 7 mm size classes. Symbols are as in figure 6-3.

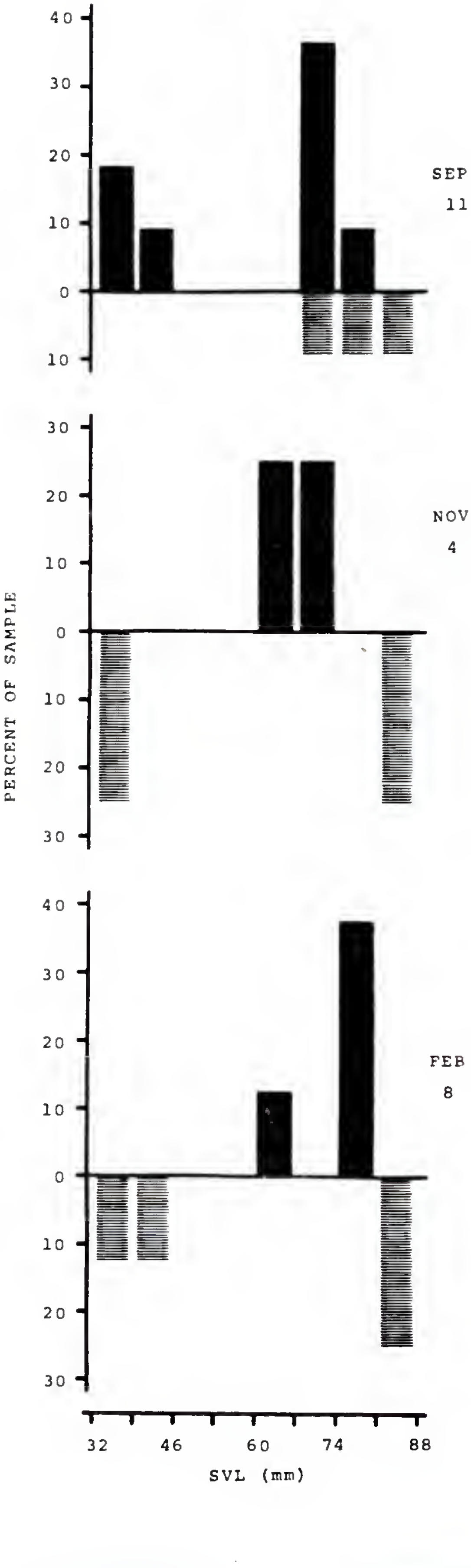

40
30
20
10
0
10
SEP
11
30
20
10
0
10
20
30
NOV
4
PERCENT OF SAMPLE
40
30
20
10
0
10
20
30
FEB
8
32
46
60
74
88
SVL (mm)

FIGURE 6-19. Seasonality of Reproductive Activity in Male *Anolis capito*. Symbols are as in figure 6-4.

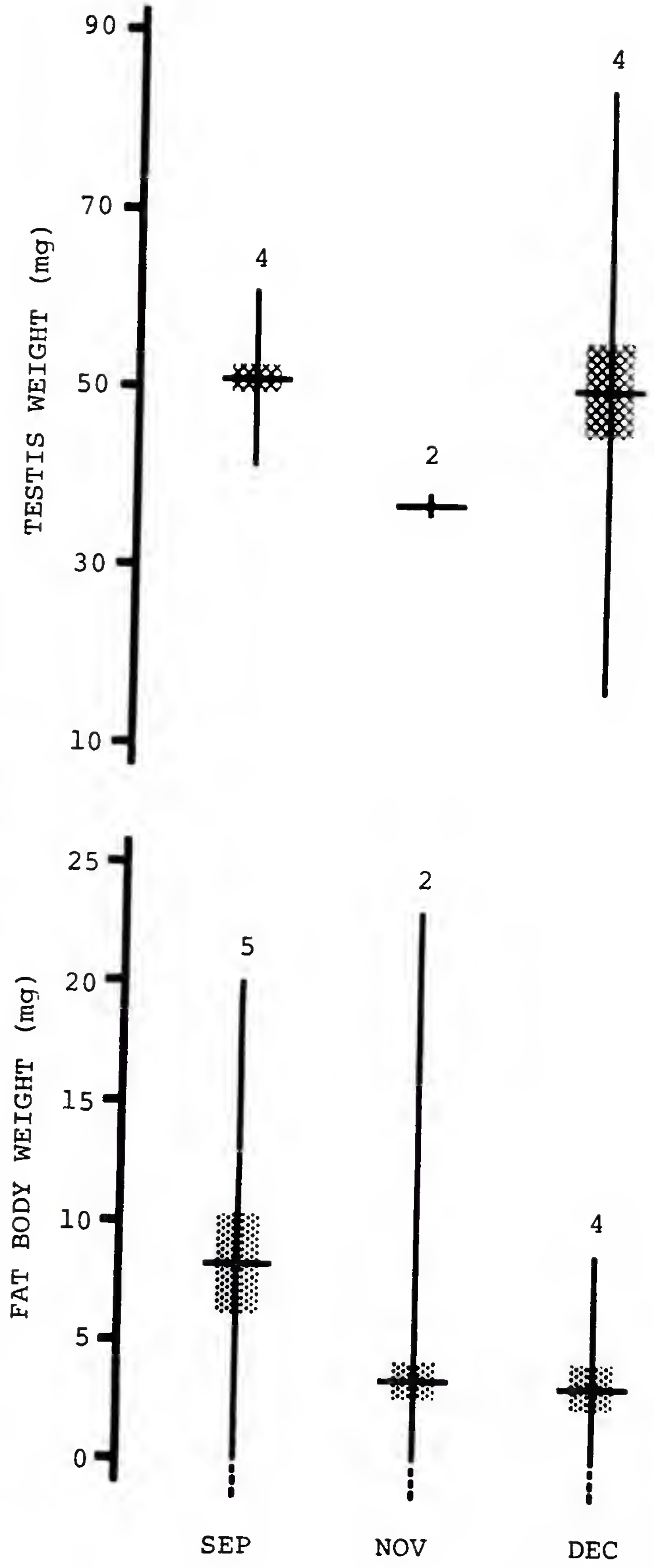

90
70
50
30
10
TESTIS WEIGHT (mg)
4
2
4
25
20
15
10
5
0
FAT BODY WEIGHT (mg)
5
2
4
SEP
NOV
DEC

FIGURE 6-20. Seasonality of Reproductive Activity in Female *Anolis biporcatus*. Lines and symbols are as in figure 6-8.

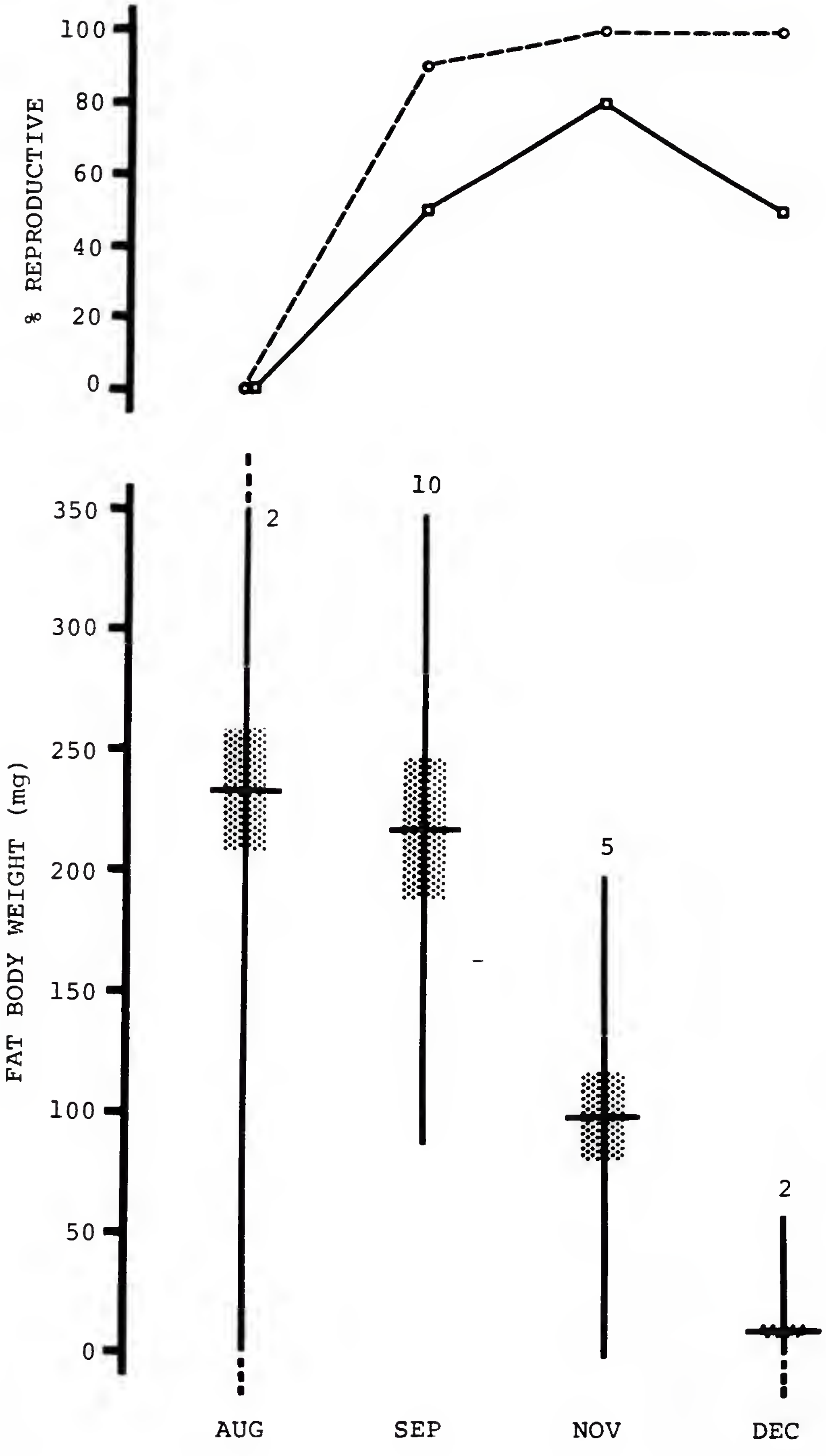

100
80
60
40
20
0
% REPRODUCTIVE
350
300
250
200
150
100
50
0
FAT BODY WEIGHT (mg)
2
10
5
2
AUG
SEP
NOV
DEC

FIGURE 6-21. Population Structure in *Anolis biporcatus*. Anoles are grouped in 7 mm size classes. Symbols are as in figure 6-3.

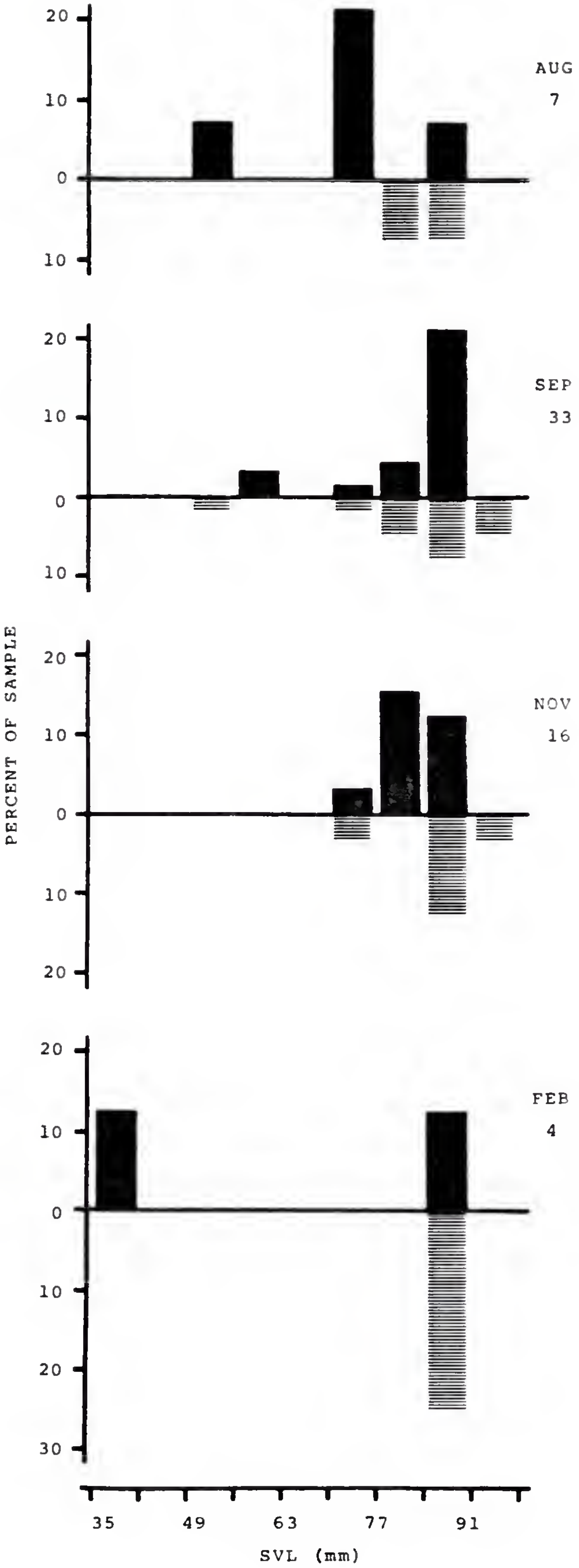

20
10
0
10
AUG
7
20
10
0
10
SEP
33
PERCENT OF SAMPLE
20
10
0
10
20
NOV
16
20
10
0
10
20
30
FEB
4
35
49
63
77
91
SVL (mm)

FIGURE 6-22. Seasonality of Reproductive Activity in Male *Anolis biporcatus*. Symbols are as in figure 6-4.

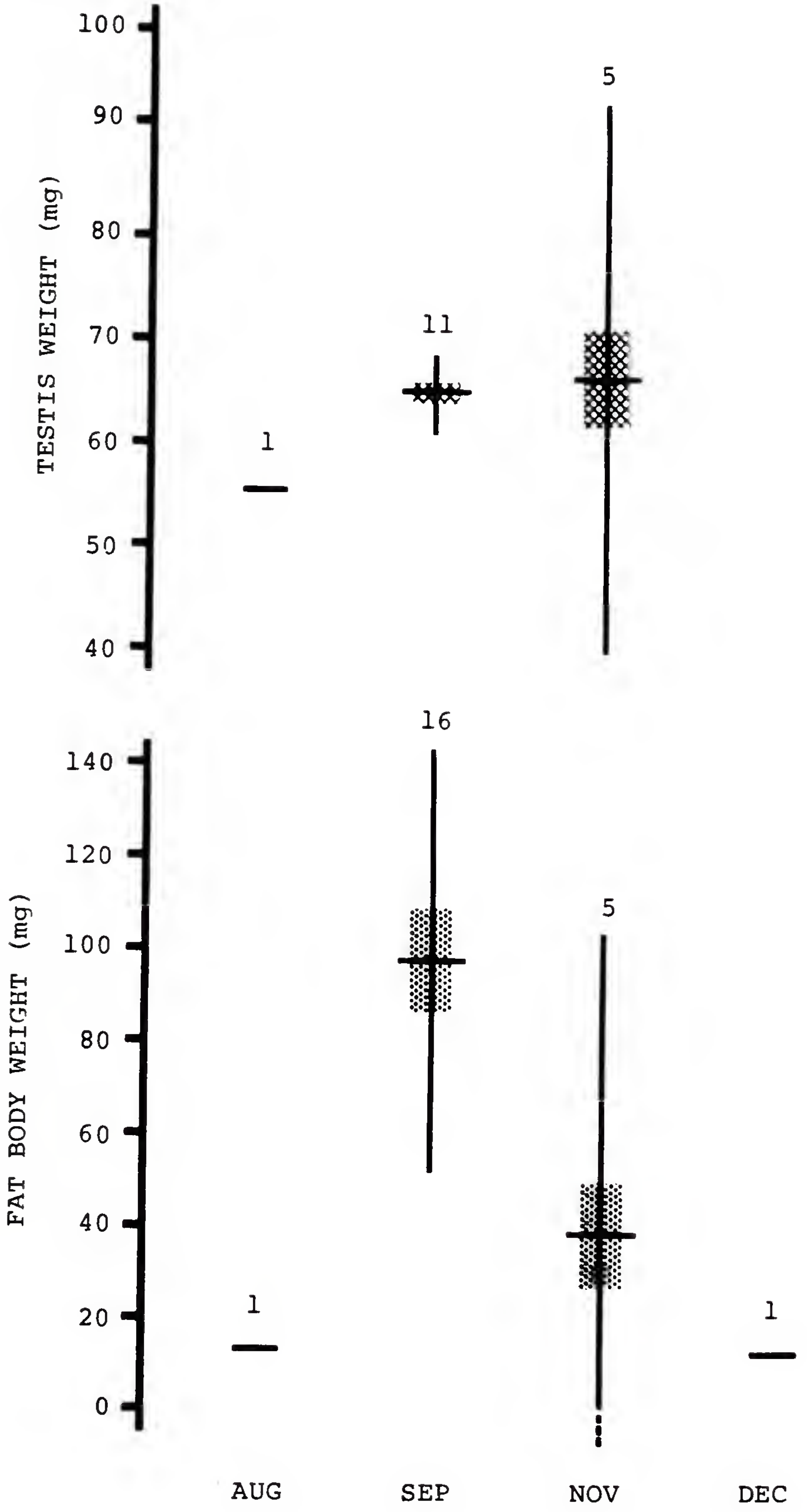

TESTIS WEIGHT (mg)
100
90
80
70
60
50
40
1
11
5
FAT BODY WEIGHT (mg)
140
120
100
80
60
40
20
0
1
16
5
1
AUG
SEP
NOV
DEC

FIGURE 6-23. Relationship Between Female Reproductive Activity and Environmental Factors.
Top: Gravidity in Female *Anolis*. Percent of sample in classes III and IV. Symbols for species are as in figure 4-1.
Next to Top: Mean Monthly Rainfall. Means (See figure 2-2.) are connected by dot and dash line. Unusual rainfall for February and May, 1970 indicated by crosses.
Center: Day Length at Río Frío, Costa Rica. Mean monthly day length for months indicated (See figure 2-2.) connected by line of hollow squares.
Next to Bottom: Daily Maximum Temperature. Means (See figure 2-3.) are connected by a dotted (solid) line.
Bottom: Daily Minimum Temperature. Means (See figure 2-3.) are connected by a dotted (hollow) line.

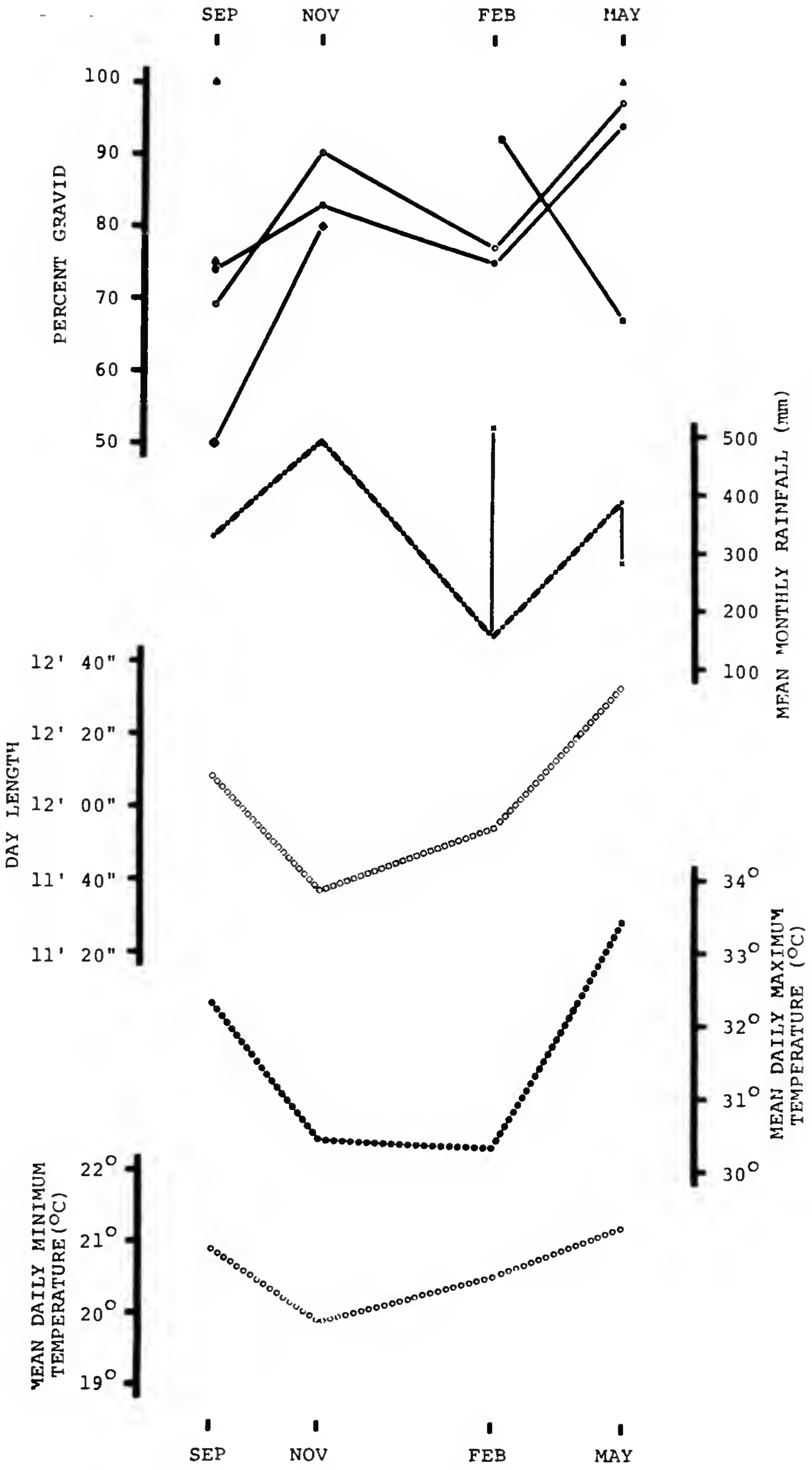
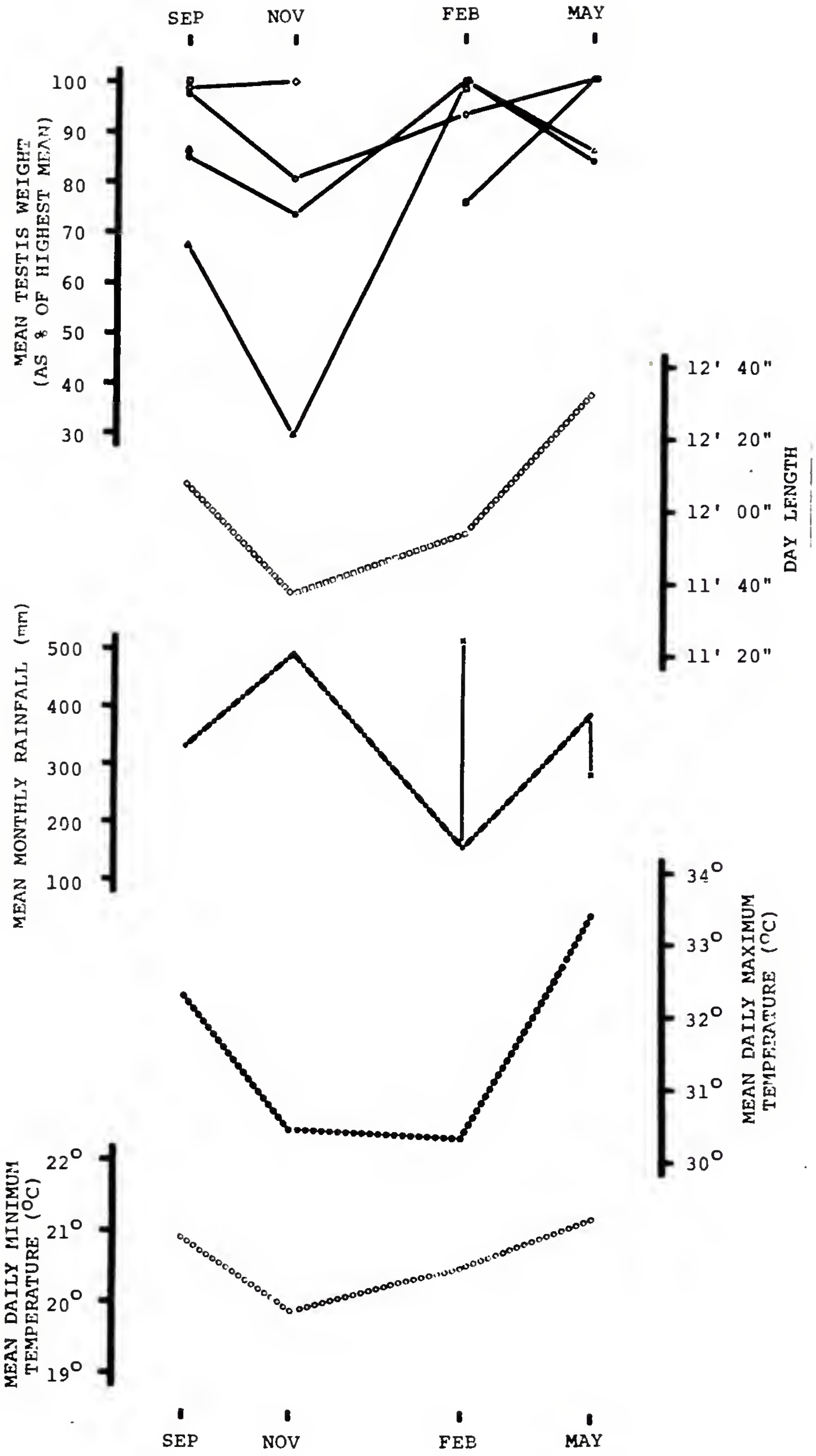

SEP
NOV
FEB
MAY
PERCENT GRAVID
100
90
80
70
60
50
MEAN MONTHLY RAINFALL (mm)
500
400
300
200
100
DAY LENGTH
12' 40"
12' 20"
12' 00"
11' 40"
11' 20"
MEAN DAILY MAXIMUM TEMPERATURE (°C)
34°
33°
32°
31°
30°
MEAN DAILY MINIMUM TEMPERATURE (°C)
22°
21°
20°
19°
SEP
NOV
FEB
MAY

FIGURE 6-24. Relationship Between Male Reproductive Activity and Environmental Factors.
Top: Testis Weight in Male *Anolis*. Mean testis weights are shown as a percent of the highest mean weight for each species. Symbols are as in figure 4-1.
Next to Top: Day Length at Río Frío, Costa Rica. As in figure 6-23.
Center: Mean Monthly Rainfall. As in figure 6-23.
Next to Bottom: Daily Maximum Temperature. As in figure 6-23.
Bottom: Daily Minimum Temperature. As in Figure 6-23.


SEP
NOV
FEB
MAY
MEAN TESTIS WEIGHT (AS % OF HIGHEST MEAN)
100
90
80
70
60
50
40
30
DAY LENGTH
12' 40"
12' 20"
12' 00"
11' 40"
11' 20"
MEAN MONTHLY RAINFALL (mm)
500
400
300
200
100
MEAN DAILY MAXIMUM TEMPERATURE (°C)
34°
33°
32°
31°
30°
MEAN DAILY MINIMUM TEMPERATURE (°C)
22°
21°
20°
19°
SEP
NOV
FEB
MAY

VII. POPULATION SIZE AND STRUCTURE

1. Introduction

Relatively few studies have been concerned with population sizes of tropical lizards. Only a few of these have determined density of anoles, and most reports of mainland anole densities are concerned with species of odd habitats. Meyer (1968) and Campbell (1973) both reported densities of semi-aquatic anoles; Jackson (1973) calculated density in a montane species, and Fleming and Hooker (1975) determined population size in a species in the severely seasonal deciduous forest of northwestern Costa Rica. Of the multitude of anole species of the lowland rain forest, only one, *A. limifrons* of Panama, has been extensively studied. Sexton and his colleagues have reported population density of that species in different seasons and at a variety of habitats (Sexton, 1967; Sexton et al., 1963, 1964; Heatwole and Sexton, 1966). In addition, Scott (1976) reported densities from "forest litter plots" for species of *Anolis*, from three localities in Costa Rica. Age and size structure of anole populations has been considered in even fewer studies. Some of the papers of Sexton and his colleagues (Sexton et al., 1963; Heatwole and Sexton, 1966) have dealt with population structure in Panamanian *A. limifrons*, and Fleming and Hooker (1975) reported population structure in *A. cupreus*. The most comprehensive paper is Fitch's (1973a) report on several Costa Rican lizards, including six species of *Anolis* from various localities and habitats.

This section includes the results of population estimation for Río Frío *Anolis* from fenced quadrats. This method of collection censuses only anoles from the forest litter up through approximately 2 m in height, thus only the ground and low bush species would be expected. Excluded because of height are *A. pentaprion*, *A. biporcatus*, *A. lemurinus* and *A. carpenteri*, though the latter two species were each collected one time in quadrats. *A. lionotus* is restricted to streamside habitats, which were avoided in placement of quadrats, and is, thus, not included. *A. capito* is not common, with only 2 individuals occurring in a single quadrat of the 20 done. Thus the fenced quadrat method served to adequately assess population size of only two species, *A. humilis* and *A. limifrons*. However, in addition to these anoles, five other lizards species and several species of amphibians were collected. These will be considered as well.

2. Materials and Methods

The method used to determine the density of anoles was the fenced quadrat method used by Sexton and his colleagues studying *A. limifrons* in Panama (Sexton, Heatwole, and Knight, 1964; Heatwole and Sexton, 1966; and Sexton, 1967), with some changes. The procedure is as described below.

During each study period, five $100 m^2$ quadrats were selected, fenced, and cleared. The site of each quadrat was selected more or less at random in an area of seemingly undisturbed forest. All quadrats were in the same general area, with later quadrats interspersed among earlier. However, no quadrat was closer than 30 m to a previous site. Sites were chosen to avoid large fallen trees, viney tangles, usually associated with open canopy areas, or excessively wet areas. Each site was selected and marked off, 10m x 10m, just after noon (Fig. 7-1A). During the early afternoon a shallow trench was dug around the perimeter and the bottom 10-15 cm of a 2m high plastic sheet was buried. The plastic fence was collapsed and folded, so as to be as inconspicuous and unobtrusive as possible. The site was then left to allow anole activity to return to normal. Early the next morning, the plastic fence was raised as quickly as possible and held in position with poles located on the outside of the fence (Fig. 7-1,B). Any bush or vines overhanging the fence were then cut. Next the quadrat was searched superficially, for obvious animals. Following this, all vegetation, excluding trees over 4 cm in diameter, was cut, searched and thrown over the fence. Large trees were cleared of vines and associated debris up to a height of 2 m. When all vegetation had been searched and removed, the leaf litter was raked, searched and removed. Any stumps or rotting logs were torn apart as much as possible and removed when possible. All amphibians and reptiles collected were preserved. At that time, usually late afternoon, the site was left, fence in place (Fig. 7-1,C). The site was revisited the next morning and searched for animals that may have been missed on the previous day.[1] The fence was then removed, and the inside edge of the trench searched for animals that had burrowed down along the inside of the plastic fence (Fig. 7-1,D).

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[1] Heatwole and Sexton (1966) and Sexton (1967) give evidence that anoles will not ordinarily enter or leave such fenced plots.

The number of animals collected in the five quadrats for each period were used to derive an estimate of population density for any repeatedly collected species of *Anolis*, for all anoles, for all lizards, for all *Eleutherodactylus*, and for all reptiles and amphibians for each period. Estimates are given as plus or munus the standard error, provided with 95% confidence intervals using the t statistic, and adjusted to a "per hectare" density (1ha=10,000m^2 =2.471A). All lizards were measured as has been described earlier, frogs were not weighed or measured, so biomass estimates are available for lizards only. Dates that quadrats were cleared are given in Table 7-1.

3. Density and Biomass of Anoles

The twenty fenced quadrats from all four period yielded 194 anoles, 60 other lizards, 15 snakes, 605 *Eleutherodactylus*, 33 other frogs and 3 salamanders, a total of 911 reptiles and amphibians in 0.2 ha. Numbers of anoles are given in Table 7-2; biomass is given in Table 7-3. Using all twenty quadrats to derive an estimate, the number of anoles of any species residing below 2 m is 688-1252/ha, with biomass of 422-1026 g/ha. Figures 7-2 and 7-3, however, indicate that there may be differences by season and by species that should be considered.

Anolis humilis.

The most abundant species of anole in 12 of 20 quadrats was the smallest, *A. humilis*. The density and biomass of this species estimated from all quadrats, is 625 ± 115 lizards/ha or 393 ± 74 g/ha. Confidence limits are 384-866 lizards/ha or 238-547 g/ha. *A. humilis* was significantly more abundant than *A. limifrons* in September and November ($P<.05$), but not in February or May.

Seasonal variation in density is apparent (Fig. 7-2, Table 7-2) for this species, with the greatest density in November (1200±281 lizards/ha) and the lowest in May (160±68 lizards/ha). These periods correspond to the end and beginning of the rainy season respectively. It appears that the low density in May is a result of a decline throughout the dry season (Fig. 7-4). Both February and May have significantly lower densities than November, and May is significantly lower than September (Table 7-4). The same trend is present with the same differences significant if biomass is considered instead of density (Fig. 7-3, Tables 7-3, 7-4).

Anolis limifrons.

The density of *A. limifrons*, estimated from all twenty quadrats, is 325±46 lizards/ha. This species was more numerous than *A. humilis* in only five of the twenty quadrats, two in February and three in May. Biomass of *A. limifrons*, estimated from all quadrats is 231±31 g/ha, confidence limits are 166-296 g/ha.

There is no significant seasonal variation in either density or biomass in *A. limifrons* (Table 7-4). Seasonal density estimates vary from a high of 360±112 lizards/ha (February) to a low of 280±66 lizards/ha (May). Biomass is lowest in November (186±69 g/ha) because a greater proportion of the lizards are immature, and highest in May (265±45 g/ha) when most *A. limifrons* are adults.

These density estimates of low bush and forest floor anoles at Río Frío are quite similar to those of Heatwole and Sexton (1966) for Barro Colorado Island populations of *A. limifrons*. They calculated a density of 1172±135 lizards/ha for *A. limifrons*, the only anole they collected. At Río Frío *A. limifrons* has a much lower density (325±46 lizards/ha), but *A. humilis* is also found there. From all anoles collected in all twenty quadrats, the estimate is 970±135 lizards/ha, not significantly different from the Barro Colorado *A. limifrons* density.

Other estimates of lowland rain forest anole numbers are much lower, but probably not as accurate. Sexton et al. (1963) obtained estimates of from 124 lizards/ha to 259 lizards/ha for *A. limifrons* in the Río Canclon area of Panama. These estimates, however, were only for lizards associated with saplings and trees; and they pointed out that most *A. limifrons* inhabited "the smaller herbs and shrubs not sampled." Scott (1976) collected *A. humilis* and *A. limifrons* in leaf litter plots at Finca La Selva, only a few kilometers from Río Frío.

He collected only 10 *A. humilis* and 8 *A. limifrons* in 19 plots of 58 m^2 each. These densities, 91 *A. humilis*/ha and 73 *A. limifrons*/ha are low probably because the plots were not fenced and the primary object was to collect animals in the litter.

Estimates of anole density from other habitats are variable. Fleming and Hooker (1975) found in excess of 1200 *A. cupreus* per ha in the Guanacaste deciduous forest during the dry season. Two lowland species of semiaquatic habitat, *A. lionotus* and *A. poecilopus,* censused in Panama by Campbell (1973), had densities of 133-1000 lizards/ha, depending on season and other variables. In contrast, Jackson (1973) estimated less than 90 *A. tropidonotus* per ha in a montane pine forest in Honduras.

Seasonal density variation, apparent in *A. humilis* but lacking in *A. limifrons* at Río Frío, has been found in other studies. Fleming and Hooker (1975) found a sharp decrease in density in *A. cupreus* during the wet season in the deciduous forest. They suggested that this might be more of a behavioral difference than a real difference in lizard numbers. A similar phenomenon was observed by Sexton et al (1963) in *A. limifrons* on a flood plain of the Río Canclon in Panama. It would be interesting to determine if this dry season increase is due to immigration from drier upland areas. In the upland populations near the Río Canclon, Sexton, et al, (1973) found a decrease in density during the dry season, such as happened in Río Frío *A. humilis*. This type of change was also shown by both of the riparian species studies by Campbell (1973).

The dry season decline in tropical anole density is usually associated with a comparable decline or cessation of egg production by adult females. (Sexton et al., 1963; Heatwole and Sexton, 1966; Campbell, 1973; Fleming and Hooker, 1975). In *Anolis humilis* at Río Frío this does not appear to be the case.

A. humilis density is reduced by two-thirds between November and February, even though 83% of the adult females were gravid in the November sample. Eggs of these females should have been contributing to the February juveniles, just as eggs from the gravid females in February (75%) should have contributed to a higher May population. Instead density continued to drop to only 13% of the November estimate. If reduction of gravidity is not responsible for the population reduction, perhaps, as suggested by Fitch (1973b), there, is a delay in egg deposition. This might account for a short term reduction in juveniles, but surely a small short-lived anole such as *A. humilis* can not retain shelled eggs for almost four months.

A more probable explanation in this case would be that there was an increase in egg or hatching (or even adult) mortality during the dry season. Ground and low-bush anoles typically deposit eggs in ground litter or cracks, holes and debris on tree trunks (Sexton et al, 1963; Fitch, 1973b) where they are subject to dessication as the litter drys out. The small size of hatchlings would make them particularly susceptible to dessication, which may explain, in part, why hatchlings of both *A. humilis* and *A. limifrons* are usually found in leaf litter. Even at Río Frío in a lowland rainforest, litter can be completely dry for several days during a normal dry season. This would undoubtedly reduce small anole and anole egg survival. Such an effect was discovered by Sexton (1967). Comparing two dry season series of fenced quadrats in the same area on Barro Colorado Island, Sexton found wide disparity in densities of *A. limifrons*. In just two years, he noted a significant drop from almost 1200 lizards/ha to only about 400/ha. This he attributed to a three year stretch of unusually dry dry seasons.

February 1970 probably had just the opposite effect, however. I suggest that the population reduction in *A. humilis* is due, at least in part, to too much water. The torrential rains of early February caused accumulation of standing water in many areas of forest floor. Eggs in floor litter and very small hatchlings might well have been drowned outright. All *A. humilis* would certainly have been exposed to reduced foraging areas for more than a week. In the February quadrats, done in the days immediately following these heavy rains, there is a significant lack of small *A. humilis* (Fig. 7-5). One test of this hypothesis would be to consider the density of a species that is less closely associated with the ground. *A. limifrons* adults normally perch above the ground and even hatchlings readily ascend the bases of trees, saplings, and herbs. Sexton et al. (1963) found 20 of 41 eggs of *A. limifrons* deposited above the ground litter. This species was not as greatly affected by the February rains as was *A. humilis*. There is no significant change in density in any period, and hatchling lizards are present in all.

4. Population Structure of Anoles

The first problem encountered in any discussion of population structure is the reliability of the sample. To be a reliable sample, the collection must include sizes and sexes in the same proportions that they occur in the population being surveyed. The most common procedure is simply to collect all or a certain number of lizards as they are encountered (Sexton et al., 1963; Heatwole and Sexton, 1966; Andrews, 1971a; Fitch 1973a). There are, of course, many factors that will cause over- or under-representation of certain classes in a sample, e.g. cryptic coloration or behavior, more obvious perch site. Purposeful attempts to "correct" these imbalances might well result in overcompensation. One way to overcome this difficulty would be to fence off an area and collect all animals in the area--just as was done with the twenty fenced quadrats.

If the quadrat samples (Fig. 7-5, 7-6) are accurate representations of the total population, are the general samples also (Fig. 6-3, 6-4)? To answer this each sample of *A. humilis* and *A. limifrons* was tested against the quadrat samples from the same period in two ways. Sex ratios were compared by 2 x 2 chi-squared tests, and in no case is there a significant difference in the proportion of males and females between the quadrant sample and the entire sample. Disregarding sex, SVL distributions were compared by Kolmogorov-Smirnov tests. In no period was there a difference for *A. humilis*, and the same is true for 3 of 4 periods for *A. limifrons*. However, in the May sample, there is a greater proportion of small lizards in the general sample than in the quadrat sample ($P<.01$).

Population structure in both *A. humilis* and *A. limifrons* has been discussed by Fitch (1973a). Fitch captured over 500 *A. humilis* at two Costa Rican sites on five dates from January to September. He found little evidence of seasonal change in population structure, only a slight reduction in the number of young in the late dry to early wet season. At Río Frío there appears to be a reduction in the number of young in the February samples (Fig. 6-3, 7-5) as discussed in the previous section. Yet when SVL distribution for quadrat samples are compared, none of the changes are significant (Kolmogorov-Smirnov test, $P>.05$). Nor are there significant changes in the proportion of males and females when quadrat samples from one period are compared to those of the next period (2 x 2 chi-squared test, $P>.05$). *A. humilis*, then does appear to fit Fitch's (1973a) Type 1 pattern, i.e, little or "no temporal change in the level of reproduction and stability has been attained" so that "all sizes and ages are constantly present in the population in unvarying ratios."

Fitch (1973a) studied *A. limifrons* in cacao groves at Turriabla, Cartago Province, and Beverly, Limón Province, Costa Rica. He described this species as showing a Type 2 pattern, i.e. "reproduction is continuous throughout the year, but its level changes in response to climatic factors in areas where there is some seasonality" so "all ages are always present but in constantly changing ratios." In his samples juveniles were few in April and May, but increased to a majority of the sample in October and November.

In at least some areas in Panama, *A. limifrons* is much closer to Fitch's Type 3, i.e. dry season cessation of breeding. Sexton et al. (1963) found a complete lack of young and gravid females in the dry season in Darien, Panama. On Barro Colorado Island, Heatwole and Sexton (1966) found a significant reduction in the number of small *A. limifrons* in their March-April collections as compared to June samples, yet egg production did continue apparently throughout the year.

At Río Frío *A. limifrons* population structure seems to lean in the other direction--toward the Type 1 pattern. Río Frío ordinarily gets considerably more dry season rainfall than Turrialba, Beverly, or either Panama locality. Presumably as a result of this, there is little seasonal change in population structure. Reproduction is variable, but continuous, and young were present in all samples. The only significant shift in SVL distribution is to more larger individuals in the May samples as compared to either the November or February quadrat samples ($P<.01$ for both, Kolmogorov-Smirnov test). This trend was not so obvious for the May general sample, in which young were represented.

For the other six species of *Anolis* at Río Frío, fenced quadrat samples are not available, yet some information can be gained from the general samples. While the above mentioned deficiencies may well apply to these samples, there are some reasons to believe that they are not always of major importance. First, in the case of the more arboreal species collected from the felled trees, the lizards tended to stay on the tree and every individual seen was pursued and usually caught. This is not always true with the more common, more terrestrial *A. humilis* and *A. limifrons*. Secondly, some of the other species are much larger and therefore less likely to escape notice. The close correspondence between the fenced quadrat samples and the general samples of *A. humilis* and *A. limifrons*, also supports the limited acceptance of the other samples. The small sample size of some species does make seasonal comparison impossible.

Two species appear to fit Fitch's Type 2 pattern. *A. lemurinus* (Fig. 6-12) has a significantly higher proportion of young in the September sample than in the May sample ($P<.01$, Kolmogorov-Smirnov test) and a significantly higher proportion of young in November than either February ($P<.05$) or May ($P<.001$). *A. lemurinus* also seems to have, though the sample is small, a definite reduction in gravidity during the dry season. This species typically inhabits the rather exposed trunks of medium to large trees, and may be more susceptible to dry season dessication. The other species with a significant dry season reduction in reproduction is *A. lionotus* (Fig. 6-16). The proportion of young was significantly less in the May sample than in any other sample ($P<.05$, SEP vs. MAY and FEB vs. May; $P<.001$ NOV vs. MAY) and less in the February sample than the November ($P<.01$). This species is apparently dependent for dry season moisture on small creeks and rivers, the flow of which may be affected by a severe dry season.

Campbell (1973) found evidence that reproduction and population structure of *A. lionotus* is reduced more in the dry season in populations along small streams than along larger ones. Rand (1967c) even suggested that hilltop populations of *A. limifrons* have a longer dry season non-reproductive period than do streamside populations where the leaf litter area is moist. Seasonal streams drying may have been the cause of the change at Río Frío, but probably not as those streams had flowing water at all times when my collections were made. A more probable cause for the period studied was flooding. Torrential rains during both December and February caused widespread flooding along most streams and rivers.[1] Such floods must certainly take a severe toll on *A. lionotus* which perches, sleeps and takes refuge in and along streams. Small individuals would not be as able to cope with fast-moving flood water as a large adult, and eggs would be easily washed away and drowned. This would produce the lack of small individuals found at Río Frío in February and May. Fitch (1973b) found evidence of severe population reduction by heavy flooding in a streamside population of *A. cupreus*. No significant differences in population structure were found in the remaining four Río Frío anoles.

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[1] Flooding was so severe that several bridges were destroyed and considerable other property damage occurred.

5. Density, Biomass and Population Structure of Other Lizards

In addition to the anoles, three other species of terrestrial lizards were found in fenced quadrats in enough numbers to provide estimates of density and biomass. Those found were a skink (*Leiolopisma cherriei*), a gecko (*Lepidoblepharis xanthostigma*), and a xantusiid (*Lepidophyma flavimaculatum*). In addition one individual each of an arboreal gecko, *Sphaerodactylus sp.* and a terrestrial, second-growth, teid, *Ameiva festiva*, were collected.

Leiolopisma cherriei is a small, terrestrial skink, found in lowland rain forests, forest edges and some disturbed situations (Fitch, 1973b). Thirty-nine of these lizards were taken at Río Frío, of which twenty-three individuals were collected in the twenty quadrats, yielding a density estimate of 115±30 skinks/ha (Fig. 7-7). The estimate of biomass is 300±75 g/ha (Fig. 7-8). This small skink was not common enough to show definite seasonal changes in population structure, however, juveniles were not found in February. Fitch (1973a, b) found a dry season cessation of reproduction in a Turrialba population, but found hatchlings and young in a March collection from Puerto Viejo.

In size, *L. cherriei* (adults up to 62 mm SVL, 4.7 g) is more than double the size of *A. humilis* and *A. limifrons* and less than half the weight of *A. capito*. Since it is a diurnal insectivore, it undoubtedly competes with these low perching anoles, but its low density and intermediate size probably reduce overlap. It is interesting to note that densities of the three diurnal ground lizards vary inversely with size; *A. humilis*, the smallest, 625±115/ha; *L. cherriei*, intermediate in size, 115±30/ha; and *A. capito*, the largest, 10±10/ha.[1]

Lepidoblepharis xanthostigma is one of the smallest lizards at Río Frío. Twenty-six of these tiny geckos were found in leaf litter, under logs and at the buttressed bases of large trees. Only sixteen specimans were collected in the fenced quadrats, for a density estimate of 80±28 geckos/ha (Fig. 7-7) and an estimated biomass of 45±16 g/ha (Fig. 7-8). Adults, young and presumed hatchlings were collected in November, February and May, so reproduction probably continues throughout the year, making this a Type 1 species in the terminology of Fitch (1973a). *L. xanthostigma* is virtually the same size as *A. humilis*, though its nocturnal habits must certainly reduce or eliminate competition between the two.

Lepidophyma flavimaculatum is a moderately large (adults up to 99.5 mm SVL, 17 g), nocturnal lizard. Thirty-four individuals were collected at Río Frío, almost all from rotting logs, decaying stumps or holes in the bases of large trees. Twenty-one were taken from the fenced quadrats for a density estimate of 105±41 lizards/ha (Fig. 7-7). This large lizard contributes greatly to the biomass with an estimated 656±272 g/ha (Fig. 7-8), over one third of the overall estimate of lizard biomass, 1728±350 g/ha. By weight more than half of the lizards collected in the November quadrats were *L. flavimaculatum.*

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[1] Only two *A. capito* were collected in quadrats, both in the same quadrat; hence a very unreliable estimate.

Fitch (1973a) describes a Type 4 lizard population as one with "a short annual breeding season resulting in production of a cohort of young" requiring "more than one year to mature" and thus "structured with several discrete annual age groups, one or more of which consist of immatures that do not participate in the breeding season." Figure 7-9 indicates that *L. flavimaculatum* belongs in this category. Males with enlarged testis[1] were collected in September (V_t=68mm^3) and November (V_t=70mm^3) and the only large male collected in May had small testis (V_t<4mm^3). Adult females are non-reproductive in September, ovarian follicles are all less than 1.6 mm in diameter. In November reproduction has commenced with follicles from 4-5mm, and by February larger follicles and unshelled oviducal eggs are present. Two adult females in the May sample each contained four embryos (Fig. 7-9) and a third contained one large (36 mm SVL) embryo and six corporea lutea indicating that some young had already been born. Another female collected

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[1] Testis volume was calculate using the formula for the volume of an ellipsoid as suggested by Mayhew (1963):

$$Vt=4/3\ (\tfrac{1}{2}L)\ (\tfrac{1}{2}D)^2=0.5236LD^2,$$

where L is the length (or longest diameter) and D is the shortest diameter at the widest part.

in May and returned to the University of Florida gave birth to two young on 2 June, 1970 (Fig. 7-9). No *L. flavimaculatum* less than 81 mm SVL was mature.

Juveniles apparently enter the population at the beginning of the rainy season (May-June). The size of the small classes increases from September through May. First reproduction probably occurs in the second year.

In size, *L. flavimaculatum* is about the same as *A. capito* and several times as large as *A. humilis*. Size difference undoubtedly reduces competition between *A. humilis* and *L. flavimcaulatum*, although the extended life and slow growth of young of the latter lessens this difference. The major factor separating this species from both terrestrial anoles is activity time. *L. flavimaculatum* appears to be strictly nocturnal.

6. Density of Frogs

Probably the major non-anole competitors of the Río Frío *Anolis* are several species of frogs. Almost 70% of the amphibians and reptiles taken from the fenced quadrats were frogs, and 95% of the frogs were members of the speciose tropical American genus *Eleutherodactylus*. All *Eleutherodactylus* were not identified to species, but most were *E. bransfordi*.

In sixteen of the twenty quadrats there were more *Eleutherodactylus* than anoles. The difference between numbers of *Anolis* and *Eleutherodactylus* was significant for each period and for all periods combined (Table 7-4). The overall estimate of *Eleutherodactylus* density is 3025±328 frogs/ha with 95%

confidence limits of 2339 to 3711/ha. In contrast, Scott (1976) found only 112 *Eleutherodactylus* in 19 58 m^2 quadrats at La Selva which would extrapolate to 1016 frogs/ha. La Selva is located only about 10 km from Río Frío is a biologically similar area. That Scott (1976) found the density of *Eleutherodactylus* only about 1/3 of that found at Río Frío is more likely a difference in technique than real difference. Scott's quadrats were not fenced in any way, and it would be quite easy for small cryptic frogs and lizards to "sneak out" as the quadrat is being cleared. If this is the case, there would seem to be less opportunity to overlook the more obvious species, such as the bright red, slow-moving *Dendrobates pumilio*. At La Selva, Scott found 32 of this species or 290/ha, more than the 145±33/ha found in the fenced quadrats at Río Frío. In a lowland rain forest on the Osa Peninsula of southwest Costa Rica, Scott found 93 *Eleutherodactylus* in 20 quadrate (802/ha); and near San Vito, an upland locality in southern Costa Rica, he found 315 in only 10 quadrate (5431/ha).

Most of the *Eleutherodactylus* and *Dendrobates pumilio* found at Río Frío were very small, less than the size of *A. humilis* and would be expected to feed on smaller insects, thus reducing overlap. The larger species of *Eleutherodactylus*, e.g. *E. biporcatus*, are much less common than their smaller congeners and, thus, have little effect on anole populations. In addition, the temporal difference is again important, most species of *Eleutherodactylus* frogs are essentially nocturnal. The same is not true of *D. pumilio*, which is diurnal and undoubtedly competes for food to some extent with small individuals of both *A. humilis* and *A. limifrons*. Low density of this species also alleviates competitive effects on the anoles.

TABLE 7-1.
Dates of Population Quadrats

S-1	20, 21 SEP 1969
S-2	24, 25 SEP 1969
S-3	25, 26 SEP 1969
S-4	29, 30 SEP 1969
S-5	30 SEP-1 OCT 1969
N-1	5, 6 DEC 1969
N-2	7, 8 DEC 1969
N-3	9, 10 DEC 1969
N-4	11, 12 DEC 1969
N-5	13, 14 DEC 1969
F-1	16, 17 FEB 1970
F-2	18, 19 FEB 1970
F-3	20, 21 FEB 1970
F-4	22, 23 FEB 1970
F-5	24, 25 FEB 1970
M-1	9, 10 MAY 1970
M-2	11, 12 MAY 1970
M-3	13, 14 MAY 1970
M-4	15, 16 MAY 1970
M-5	17, 18 MAY 1970

TABLE 7-2.
Numbers of Amphibians and Reptiles Collected in Fenced Quadrats

GROUP	QUADRAT	SEP	NOV	FEB	MAY	
Anolis humilis	1	6	19	1	0	
	2	7	6	4	3	
	3	11	11	7	0	
	4	7	6	5	2	
	5	5	18	4	3	ALL
	Mean	7.20	12.00	4.20	1.60	6.25
	S.D.	2.28	6.28	2.17	1.52	5.16
	95% C.I.	4.37-10.03	4.20-19.80	1.51-6.89	-0.28-3.48	3.84-8.66
Anolis limifrons	1	6	4	0	2	
	2	5	5	5	1	
	3	3	0	2	5	
	4	0	2	5	3	
	5	2	6	6	3	ALL
	Mean	3.20	3.40	3.60	2.80	3.25
	S.D.	2.39	2.41	2.51	1.48	2.07
	95% C.I.	0.24-6.16	0.41-6.39	0.48-6.72	0.96-4.64	2.28-4.22
All *Anolis*	1	12	23	1	2	
	2	12	11	9	4	
	3	17	11	9	5	
	4	7	9	10	5	
	5	7	24	10	6	ALL
	Mean	11.00	15.60	7.80	4.40	9.70
	S.D.	4.18	7.27	3.83	1.52	6.03
	95% C.I.	5.81-16.19	6.58-24.62	3.04-12.56	2.52-6.28	6.88-12.52
All Lizards	1	12	33	1	2	
	2	13	18	11	7	
	3	18	14	11	10	
	4	7	11	14	7	
	5	12	35	10	9	ALL
	Mean	12.40	22.20	9.40	7.00	12.75
	S.D.	3.91	11.08	4.93	3.08	8.45
	95% C.I.	7.54-17.26	8.45-35.95	3.28-15.52	3.17-10.83	8.80-16.70

TABLE 7-2 - extended

All *Eleutherodactylus*	1	17	26	28	16	
	2	7	29	43	24	
	3	48	47	52	20	
	4	39	33	8	22	
	5	46	28	16	56	ALL
	Mean	31.40	32.60	29.40	27.60	30.25
	S.D.	18.37	8.44	18.27	16.15	14.66
	95% C.I.	8.60-54.20	22.12-43.08	6.72-52.08	7.55-47.65	23.39-37.11
Dendrobates pumilio	1	2	6	0	2	
	2	1	0	3	0	
	3	2	1	0	2	
	4	0	1	2	2	
	5	1	1	3	o	ALL
	Mean	1.20	1.80	1.60	1.20	1.45
	S.D.	0.84	2.39	1.52	1.10	1.47
	95% C.I.	0.16-2.24	-1.17-4.77	-.29-3.49	-.17-2.57	0.76-2.14
All Amphibians and Reptiles	1	31	69	29	21	
	2	21	48	60	32	
	3	69	64	63	33	
	4	47	45	28	32	
	5	60	66	30	65	ALL
	Mean	45.60	58.40	42.00	36.60	45.65
	S.D.	19.84	11.06	17.85	16.62	17.37
	95% C.I.	20.96-70.24	44.67-72.13	19.84-64.16	15.96-57.24	37.53-53.78

TABLE 7-3.
Biomass (g) of Lizards Collected in Fenced Quadrats

GROUP	QUADRAT	SEP	NOV	FEB	MAY	
Anolis humilis	1	4.14	10.28	0.52	0	
	2	4.71	5.08	3.41	1.60	
	3	8.08	6.70	5.10	0	
	4	2.82	3.62	3.25	0.67	
	5	1.82	12.17	2.24	2.36	ALL
	Mean	4.31	7.57	2.90	0.93	3.93
	S.D.	2.39	3.57	1.68	1.04	3.30
	95% C.I.	1.35-7.28	3.13-12.01	0.82-4.99	-0.36-2.21	2.38-5.47
Anolis limifrons	1	4.01	2.16	0	2.32	
	2	2.35	3.74	3.48	1.38	
	3	3.35	0	1.63	4.17	
	4	0	0.62	2.99	2.57	
	5	1.63	2.76	4.22	2.81	ALL
	Mean	2.27	1.86	2.46	2.65	2.31
	S.D.	1.56	1.54	1.67	1.01	1.38
	95% C.I.	0.33-4.21	-0.05-3.76	0.39-4.54	1.40-3.90	1.66-2.96
All *Anolis*	1	8.15	12.44	0.52	2.32	
	2	7.06	8.82	6.89	2.98	
	3	30.54	6.70	6.73	4.17	
	4	2.82	5.14	6.24	3.24	
	5	3.45	14.93	6.46	5.17	ALL
	Mean	10.40	9.61	5.37	3.58	7.24
	S.D.	11.48	4.04	2.72	1.11	6.45
	95% C.I.	-3.85-24.66	4.59-14.63	1.99-8.75	2.20-4.96	4.22-10.26
All Lizards	1	8.15	66.37	0.52	6.47	
	2	7.06	19.18	7.91	28.20	
	3	33.18	15.35	10.21	12.56	
	4	2.82	22.07	17.78	7.30	
	5	23.31	41.31	6.46	9.30	ALL
	Mean	14.90	32.86	8.58	12.77	17.28
	S.D.	12.82	21.24	6.27	8.94	15.66
	95% C.I.	-1.02-30.82	6.49-59.22	0.79-16.36	1.67-23.87	9.95-24.61

TABLE 7-4.
Significance of Differences of Mean Numbers And Mean Biomass of Animals in Population Quadrats

	NUMBERS		BIOMASS	
	t	Sig.		
A. humilis				
SEP vs NOV	1.606	n.s.	1.697	n.s.
FEB	2.131	n.s.	1.079	n.s.
MAY	4.570	P<.01	2.900	P<.05
NOV vs FEB	2.623	P<.05	2.647	P<.05
MAY	3.599	P<.01	3.993	P<.01
FEB vs MAY	2.194	n.s.	2.229	n.s.
A. limifrons				
SEP vs NOV	0.132	n.s.	0.418	n.s.
FEB	0.258	n.s.	0.186	n.s.
MAY	0.318	n.s.	0.457	n.s.
NOV vs FEB	0.129	n.s.	0.591	n.s.
MAY	0.474	n.s.	0.959	n.s.
FEB vs MAY	0.614	n.s.	0.218	n.s.
A. humilis vs *A. limifrons*				
SEP	2.708	P<.05	1.598	n.s.
NOV	2.859	P<.05	3.284	P<.05
FEB	0.404	n.s.	0.415	n.s.
MAY	1.265	n.s.	2.653	P<.05
ALL	2.413	P<.05	2.025	P<.05
Eleutherodactylus spp.				
SEP vs NOV	0.133	n.s.		
FEB	0.173	n.s.		
MAY	0.347	n.s.		
NOV vs FEB	0.356	n.s.		
MAY	0.614	n.s.		
FEB vs MAY	0.165	n.s.		
Eleutherodactylus spp. vs. *Anolis* spp.				
SEP	2.421	P<.05		
NOV	3.412	P<.01		
FEB	2.587	P<.05		
MAY	3.198	P<.05		
ALL	5.798	P<.001		

FIGURE 7-1. Clearing Fenced Population Quadrats.
A through D, sequence of clearing fenced quadrats to determine population size:
- A. Before disturbing area.
- B. Fence in place, collapsed for night.
- C. Fence in place, collecting in progress.
- D. Collection completed, fence removed.

A, above; B, below

C, above; D, below

FIGURE 7-2. Density of Lizards from Fenced Quardats. *Anolis limifrons*, white; *Anolis humilis*, cross hatching; other species of *Anolis*, stippled; non-*Anolis* lizards, solid black.

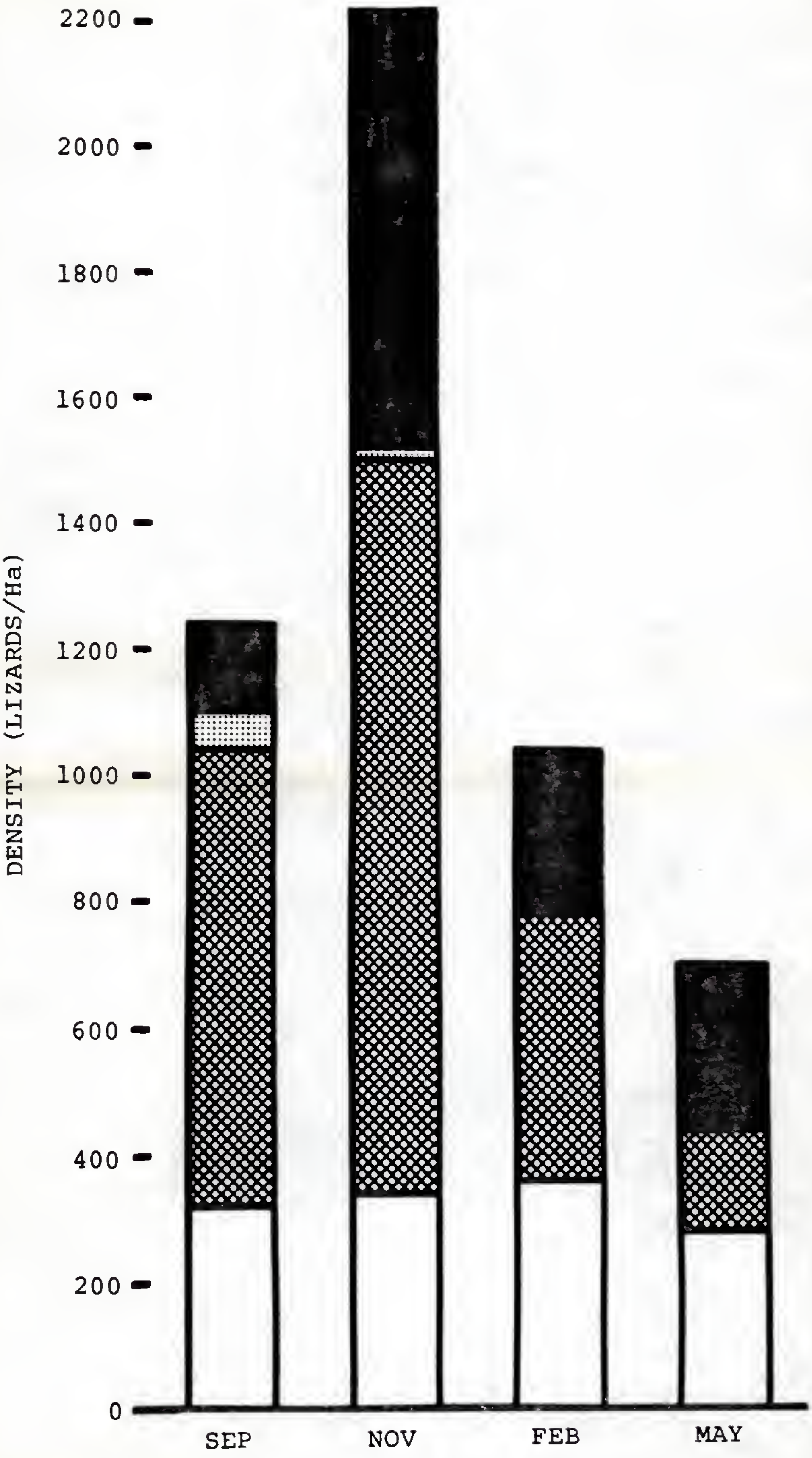

DENSITY (LIZARDS/Ha)
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
SEP
NOV
FEB
MAY

FIGURE 7-3. Biomass of Lizards from Fenced Quadrats. Bars are as in figure 7-2.

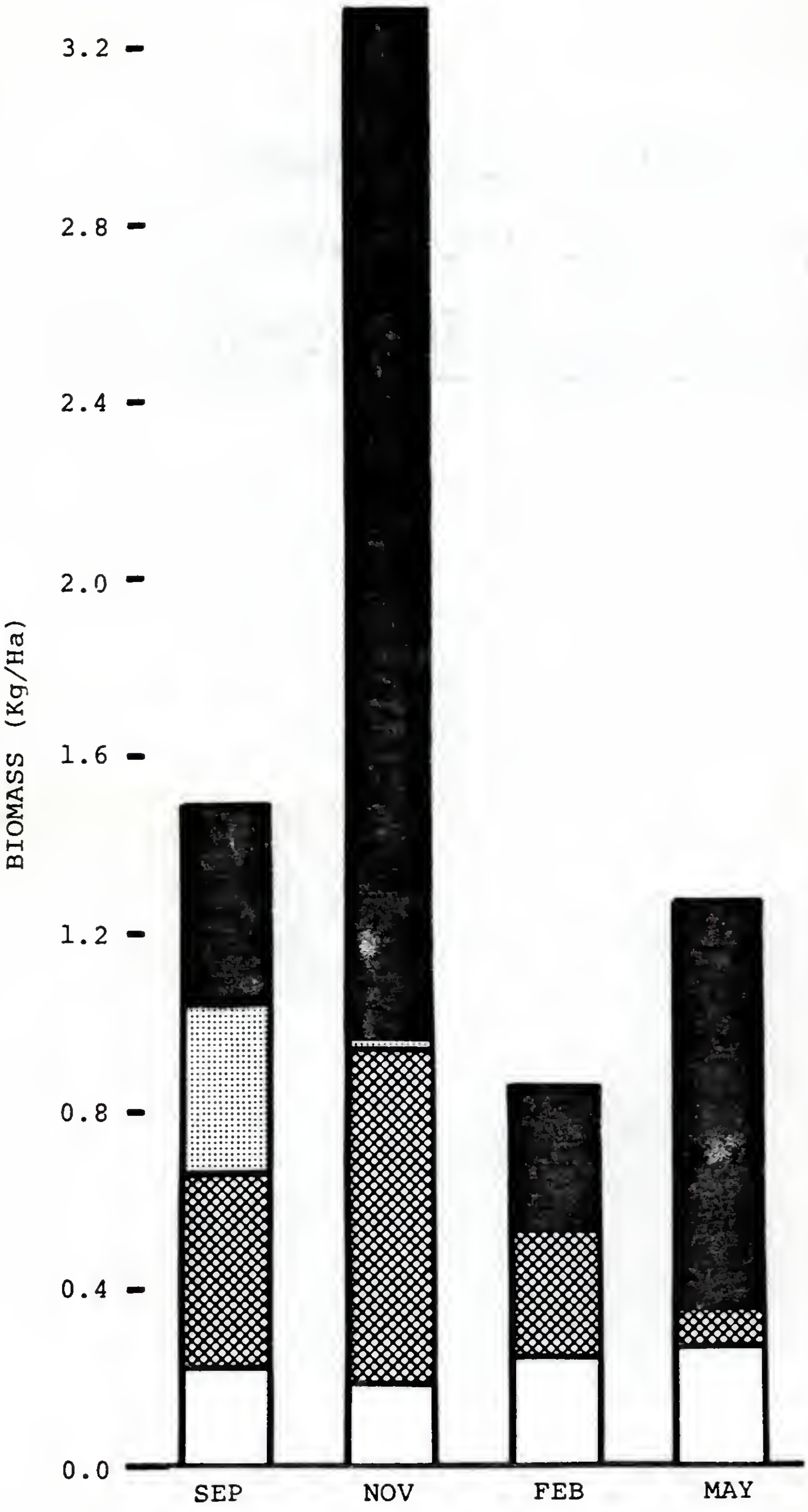

3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0.0
BIOMASS (Kg/Ha)
SEP
NOV
FEB
MAY

FIGURE 7-4. Confidence Limits on Seasonal Density Estimates. Confidence limits (95%) indicated by vertical lines; means indicated by square connected by solid line (*Anolis humilis*) or circles connected by dashed line (*Anolis limifrons*).

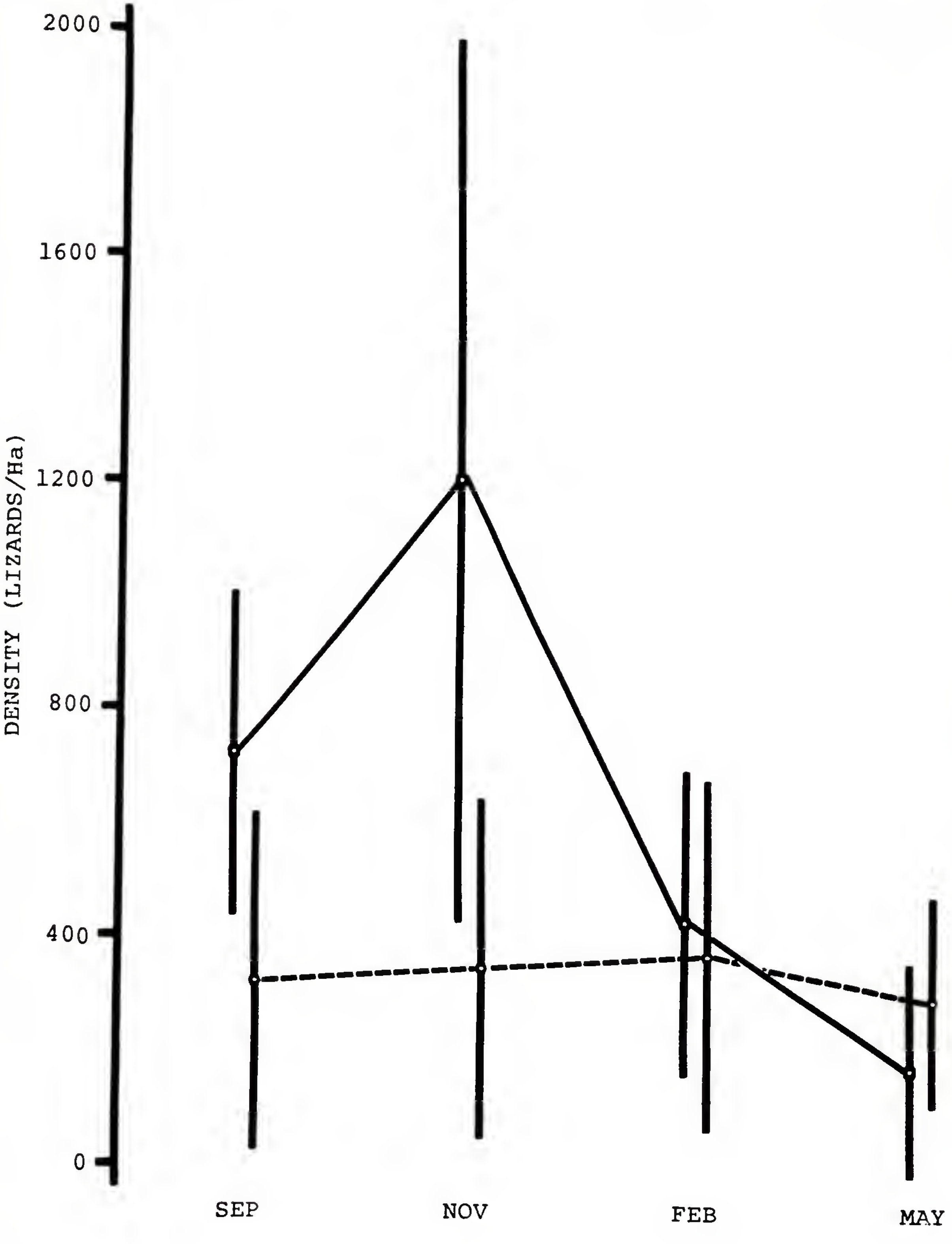

DENSITY (LIZARDS/Ha)
2000
1600
1200
800
400
0
SEP
NOV
FEB
MAY

FIGURE 7-5. Population Structure of *Anolis humilis* from Fenced Quadrats. Arrangement and symbols are as in figure 6-3.

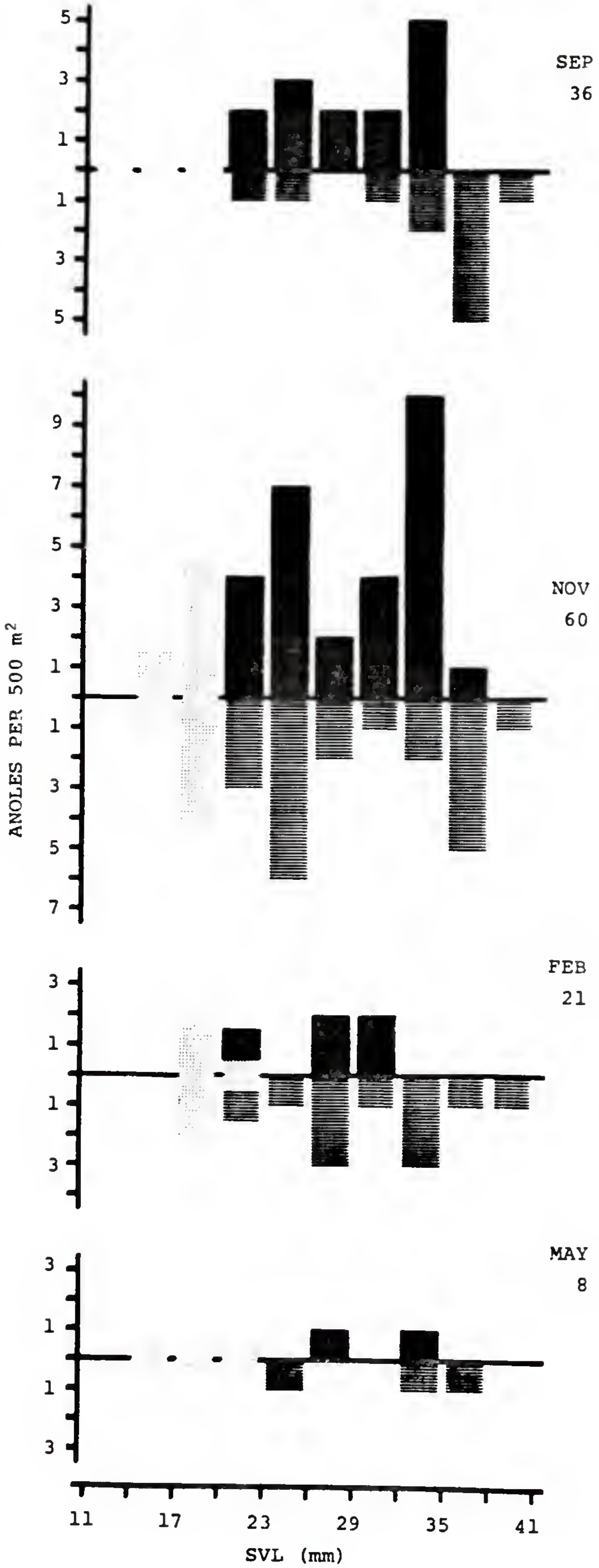

5
3
1
1
3
5
SEP
36
9
7
5
3
1
1
3
5
7
NOV
60
ANOLES PER 500 m²
3
1
1
3
FEB
21
3
1
1
3
MAY
8
11
17
23
29
35
41
SVL (mm)

FIGURE 7-6. Population Structure of *Anolis limifrons* from Fenced Quadrats. Arrangement and symbols are as in figure 6-3.

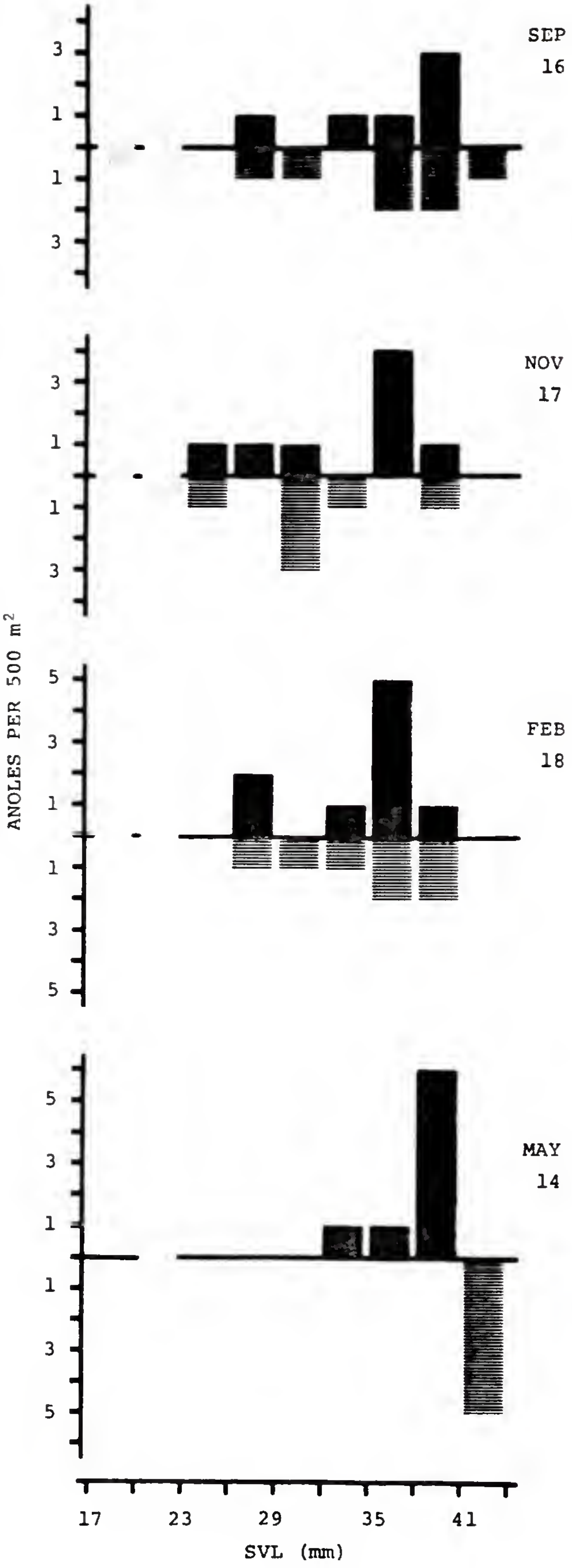

SEP
16
NOV
17
FEB
18
MAY
14
ANOLES PER 500 m²
3
1
1
3
5
17
23
29
35
41
SVL (mm)

FIGURE 7-7. Density Estimates for All Lizards. Estimated from all twenty quadrats combined, 95% confidence limits indicated by vertical lines, means indicated by circles.

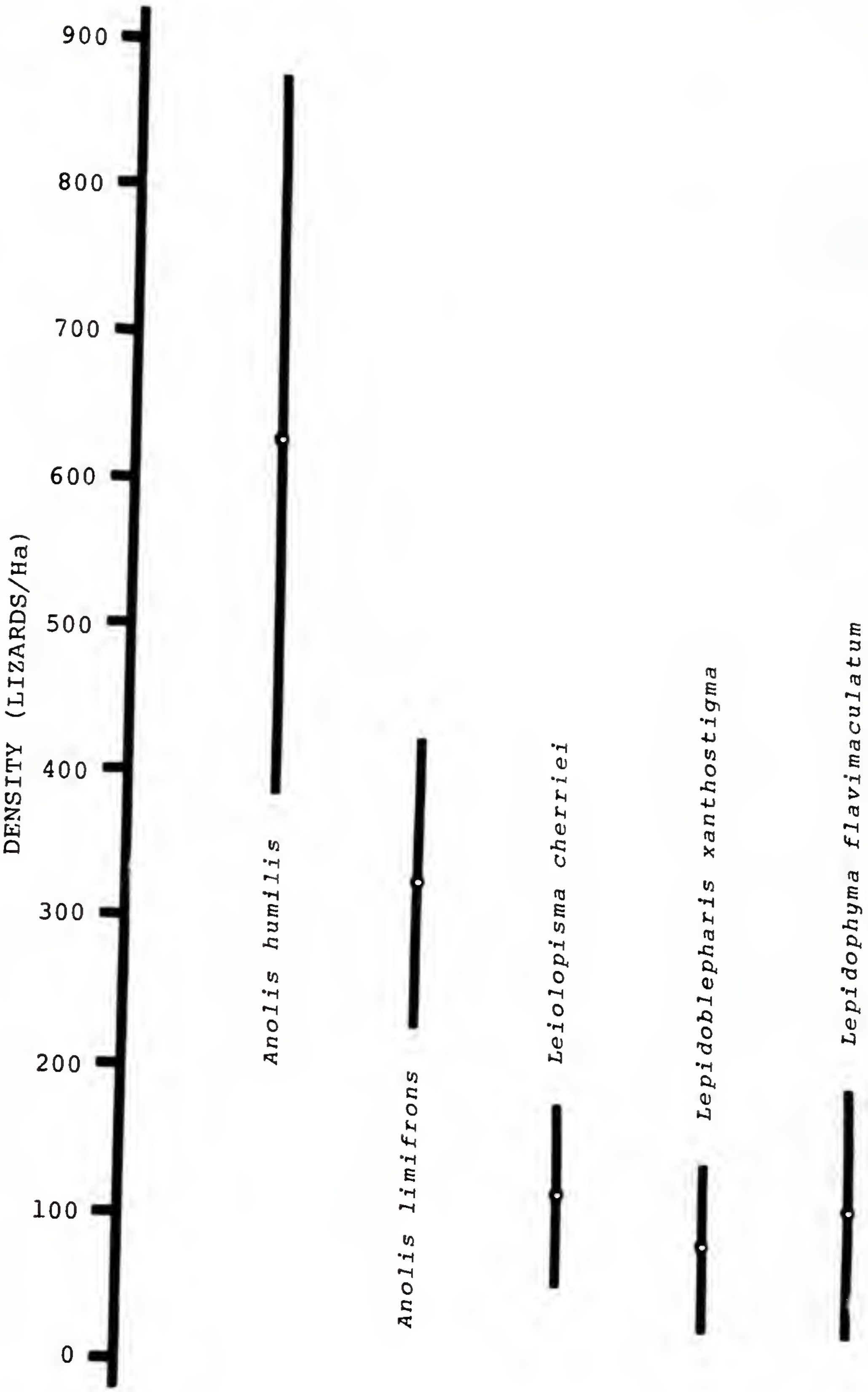

DENSITY (LIZARDS/Ha)
900
800
700
600
500
400
300
200
100
0
Anolis humilis
Anolis limifrons
Leiolopisma cherriei
Lepidoblepharis xanthostigma
Lepidophyma flavimaculatum

FIGURE 7-8. Biomass Estimates for All Lizards. Arrangement as in figure 7-7.

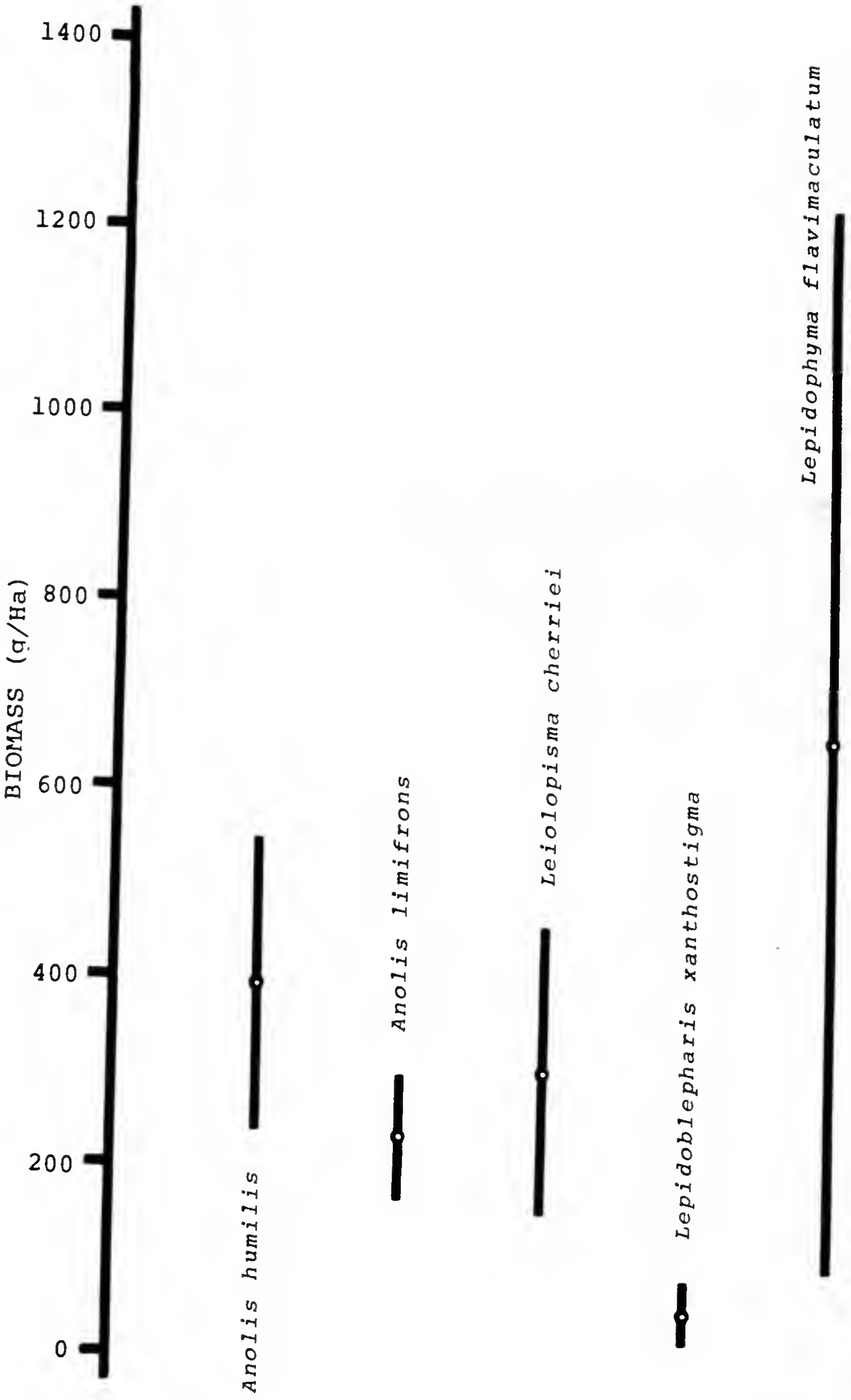
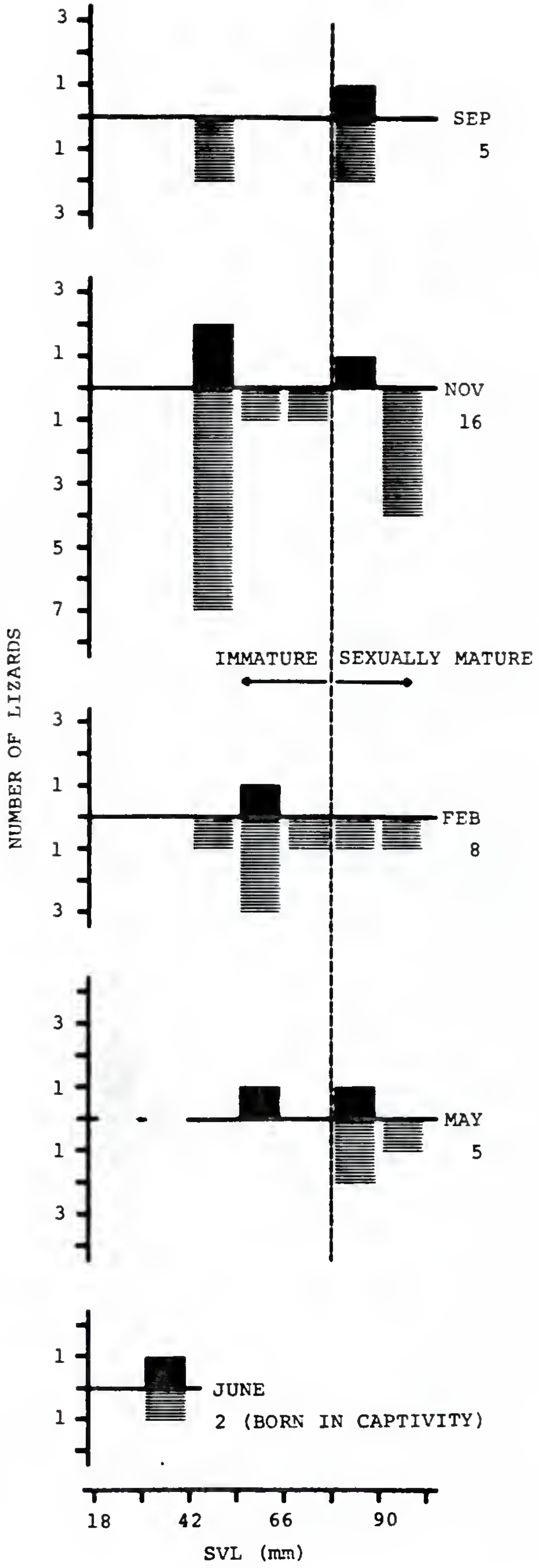

BIOMASS (g/Ha)
0
200
400
600
800
1000
1200
1400
Anolis humilis
Anolis limifrons
Leiolopisma cherriei
Lepidoblepharis xanthostigma
Lepidophyma flavimaculatum

FIGURE 7-9. Population Structure of *Lepidophyma flavimaculatum.* Includes all specimens collected at Rio Frio and 2 born in captivity at the University of Florida in June 1970. Lizards are grouped in 12 mm size classes. Black bars represent males, striped bars females, and stippled bars unsexed embryos. Sample size, embryos excluded, is given below the period designation.


NUMBER OF LIZARDS
3
1
1
3
SEP
5
3
1
1
3
5
7
NOV
16
IMMATURE
SEXUALLY MATURE
3
1
1
3
FEB
8
3
1
1
3
MAY
5
1
1
JUNE
2 (BORN IN CAPTIVITY)
18
42
66
90
SVL (mm)

VIII. SUMMARY AND CONCLUSIONS

The anole fauna at Río Frío, a site in a lowland tropical rain forest of Costa Rica, consists of eight species, *Anolis biporcatus, A. capito, A. carpenteri, A. humilis, A. lemurinus, A. limifrons, A. lionotus,* and *A. pentaprion.* Ecological separation is achieved primarily through spatial differences, both vertical and horizontal, and size difference. Dietary differences are seen as a result of these.

The co-occurrence of eight sympatric, congeneric species of over-lapping size would seem to violate the size distribution principles established by Hutchinson (1959), Schoener (1967, 1968, 1969a, 1969b, 1969c, 1970) and others, that species should differ in body size by a factor of 1.5 to 2. However, consideration of these species in subgroups by habitat shows an interesting conformation to that previously described pattern. Where one species is unaccompanied by congeners, e.g. *A. lionotus* in the terrestrial, streamside habitat, size approaches that which Schoener (1967, 1968, 1969c) found in solitary island anoles; and like those, males are larger than females. Where two species share a habitat, they diverge in size as expected, *A. capito* being just over twice the size of *A. humilis* with which it shares the ground and tree bases, and, in the tree crowns, *A. pentaprion* being just under twice as long as *A. carpenteri*. It is suggested that neither pair is separated by exactly the ratio predicted because of the competitive influence of species from the adjacent trunk habitat. *A. humilis* is smaller than the model suggests because it also competes with *A. limifrons* which is only slightly larger, and *A. pentaprion* is smaller than expected because of the peripheral influence of the largest Río Frío anole, *A. biporcatus*.

One result of the abundance of species in the Río Frío anole community is a decrease in male size. In typical anoles, males are larger than females. This is seen by Schoener as an adaptation designed for wider species exploitation of available food resources. At Río Frío most species are "surrounded" in size by other sympatric congeners. Any spread of size in a species would bring increased competition with another anole. The only two exceptions to this are *A. lionotus* and *A. pentaprion*. *A. lionotus* is, in a sense, a solitary anole. It lacks congeneric competition in its riparian habitat, thus it is able to expand its size range, and therefore the size range of prey exploited, by sexual dimorphism in size. To a lesser extent the same is true of *A. pentaprion*. It has little congeneric competition in the exposed tree crowns. In the other six species, where there is sexual size difference, it is the egg-carrying female that is larger.

Schoener (1968) and Schoener and Gorman (1968) have suggested that species in a complex anole fauna will divide food resources by prey size. Examination of stomach contents of Río Frío anoles has shown the hypothesis of discrete food usage by each species to be substantiated when restricted to habitat groups. With only one exception, prey size seems to be directly related to anole body size--the larger the lizard species the larger the prey. When species of similar sizes are compared, there is little difference in food size. Within a habitat however, each species has a preference for different sized prey (Fig. 5-26) which seems to be only a reflection of the 1.5 to 2 fold difference in body size discussed above. The species which shows the greatest deviation from the expected is, again, *A. lionotus*. These streamside anoles enjoy a certain freedom from congeneric competitive pressure, allowing them to feed on the most abundant items which are smaller than another Río Frío species of that size would eat.

Overlap, but not similarity, is greater between two large species than two small. This is because the items used by both are the least abundant large items. This increased competition between larger species might serve to push body size of larger species farther apart that are those of smaller species. As discussed above, this seems to be the rule in most anole faunas.

This separation of the species by size of items is much more pronounced than separation by taxa of prey. A few species do seem to prefer certain prey taxa or, more likely, prey forms. *A. pentaprion* feeds on flying insects in the exposed tree crown, while *A. humilis* eats a greater proportion of isopods in the floor litter; and *A. biporcatus* eats many beetles on the tree trunks. But interspecific competition, whether measured as prey similarity or overlap, is much greater for prey taxa than prey length.

Within a species, some *Anolis* show significant differences in size of prey used by different lizard sizes or sexes (Schoener 1967, 1968; Schoener and Gorman, 1968). At Río Frío, prey size does increase as predator size increases, more or less in the linear relationship predicted by Schoener (1970). When interspecies size classes are compared, there is a tendency for adults of most species to feed on larger items than juveniles, but few of these differences are significant, and certainly not as great as expected from other studies. It is suggested that this is due to the greater number of species and the lesser intraspecies size divergence in Río Frío anoles when compared to previously studied anole communities. When overlap and similarity are calculated, both are greater between classes within a species than between different species.

Overlap of prey by size is much greater between classes of large species than small species, but similarity of prey by size is not. Overlap takes into account the abundance of prey, which similarity does not. As a result interclass comparisons for large species often show the same amount of similarity as for small species, but the items of common use are the less abundant large items, hence, a higher overlap value. This would indicate a greater potential for intraspecies food competition within large species than within small.

In most species of anoles at Río Frío, there is little difference in prey length between adult males and females. In only two species, *A. pentaprion* and *A. carpenteri*, is there a significant difference between mean prey length. This is in contrast to other studies that have found differences; but in these, there was usually significant sexual size difference. In most Río Frío anoles, sizes of sexes are similar, and prey sizes are similar. Females did, however, have a higher number of items per stomach for a greater food volume per stomach. This is seen as a response to greater caloric need for egg production.

In the anoles of Río Frío, there is less competition for food between species than between classes of the same species. There is greater similarity of both prey size and taxa within than between species, and greater overlap of prey taxa within species. As stated above, it appears that, at least for a Río Frío anole, the other anole most likely to try to capture the same prey item will be another member of the same species, not of another species.

Seasonal differences in food could be considered in only the most abundant species, *A. humilis* and *A. limifrons* when compared to those from any other period. This seems to explain a seasonal difference in body weight. The May weight-length regression curve is lower than that of any other period for four species considered. This indicates a lower weight at any body length. In *A. limifrons*, at least, a smaller animal is more likely to have an empty stomach than is a larger individual. This is reflected by the high exponents of the

May weight-length regressions. The high curvature of the regression indicated that larger individuals are not as lean as smaller individuals.

Río Frío anoles are spread out in prey usage, so that when prey utilization by the entire anole community is considered, use is very similar to availability. By length, the anoles utilize most prey classes in slightly greater proportion than abundance, except for the smallest prey, which are underutilized. By taxa, use is also similar to availability, but some classes are under-represented in anole diets (ants, especially) and a few are over-represented, e.g. caterpillars, spiders and beetles. It appears, then that the anole fauna at Río Frío is composed of species of sufficient dietary diversity to take advantage of all arthropods available just as they are available, with the exception of very small arthropods and ants. Inclusion of a ninth species in the community would seem to deprive another of its food supply, or neccessitate the newcomers being very small and/or specializing on ants.

Reproduction in Río Frío *Anolis* is continuous throughout the year. There is some variation in some species, apparently in response to environmental change, but in none is there a complete cessation of reproduction. Young are present in all seasons. All should be considered as Type 1 or Type 2, tending toward Type 1, in the reproduction-population structure classification of Fitch (1973a).

Female reproduction seems to be regulated by rainfall as others have found in middle American anoles (Sexton et al, 1971;

Fitch, 1973b; Fleming and Hooker, 1975). In most, if not all, Río Frío anoles there is some reduction in egg production during both the *veranillo* and the February-March dry season. In some, e.g. *A. limifrons*, there is an obvious reduction in the number of small individuals in the May population.

A seasonal cycle in testis size is found in most anoles previously studies (Licht and Gorman, 1970). Such a cycle is found in all Río Frío anole species, but the size differences are not as pronounced as those in anoles in more obviously seasonal environments. Testis size seems to be controlled by photoperiod, though experimental evidence, presently lacking for these species, would certainly be desirable for substantiation of this hypothesis. The single annual decrease in testis weight occurs as days are decreasing in length, and the testis weight increase commences soon after daylength begins to increase. Maximal testis size, during the dry season, thus precedes maximal egg production at the beginning of the wet season.

Density of low bush and ground amphibians and reptiles at Río Frío was estimated from fenced quadrats. For all species collected in twenty quadrats density is 3752-5378 individuals/ha (95% confidence limits). Anoles, specifically two species - *A. humilis* and *A. limifrons*, comprise a major part of the herpetofauna with a combined estimate of 688-1252 anoles/ha. These are by far the most abundant reptiles, but the small *Eleutherodactylus* frogs are even more dense, 2339-3711 frogs/ha.

The most abundant anole is *A. humilis*, 384-866 lizards/ha, but numbers of this species were greatly reduced in February and May samples, possibly by flooding. *A. limifrons* had a relatively stable population density in all seasons. Means varied from 280 anoles/ha to 360 anoles/ha with an overall estimate of 228-422 lizards/ha. The May decrease in that species seemed due to decreased egg production in the dry season.

Other lizards were relatively rare in the quadrats: *Leiolopisma*, 101-129 skinks/ha; *Lepidoblepharis*, 67-93 geckos/ha; and *Lepidophyma*, 86-124 lizards/ha. One, however, contributed greatly to the biomass. Anoles had a combined estimated biomass of 422-1026 g/ha, while *Lepidophyma*, a large, nocturnal lizard, had an estimated biomass of 529-783 g/ha. Other lizards probably have little direct competitive effect on anoles, because of size, habitat or activity time differences.

APPENDICES

1. Definitions of Morphological Counts and Measurements

Measurements made on some or all anoles considered are defined as follows:

head depth: "...from the center of the vertical plane whose upper edge is marked by the posterior margin of the frontal bones as indicated by a ridge in the preserved animal."
(Schoener, 1968)

head length: "...the distance from the anterior edge of the ear opening to the tip of the snout."
(Schoener, 1968)

hear width: "...the horizontal line joining the angles of the jaw."
(Schoener, 1968)

hind leg length: "...from the anterior insertion of the thigh to the tip of the toenail of the longest toe with the leg extended at right angles to the body."
(Collette, 1961)

snout-vent length: the straight line distance from the tip of the snout to the anal opening.

subdigital lamellae: "...the number of lamallae under phalanges ii and iii of the 4th toe (the dilated portion of the toe includes all of the phalanx ii and part of phalanx iii)..."
(Williams, 1963)

tail length: the distance from the anal opening to the tip of the tail.

2. Specimens Used

Listed here are the lizards used in this study. All were collected at Río Frío, Heredia Province, Costa Rica. Numbers beginning with "UF" are Florida State Museum catalog numbers, others are the author's field numbers. All specimens are deposited at the Florida State Museum.

Anolis biporcatus

UF 30522	♂	5	August	1969
UF 30529	♂	5	August	1969
UF 30530	♂	5	August	1969
UF 30532	♀	6	August	1969
UF 30533	♀	6	August	1969
UF 30534	♂	6	August	1969
UF 30535	♂	6	August	1969
UF 30721	♂	8	September	1969
UF 30730	♂	9	September	1969
UF 30731	♂	9	September	1969
UF 30732	♂	9	September	1969
UF 30733	♀	9	September	1969
UF 30855	♂	21	September	1969
UF 30856	♀	21	September	1969
UF 30857	♀	21	September	1969
UF 30901	♂	1	October	1969
UF 30902	♂	1	October	1969
UF 30903	♀	1	October	1969
UF 30904	♀	1	October	1969
UF 30932	♂	2	October	1969
UF 30933	♂	2	October	1969
UF 30934	♀	2	October	1969
UF 30935	♀	2	October	1969
UF 30936	♀	2	October	1969
UF 30962	♂	3	October	1969
UF 30963	♂	3	October	1969
UF 30964	♀	3	October	1969
UF 30997	♂	4	October	1969
UF 30998	♂	4	October	1969
UF 30999	♂	4	October	1969
UF 31000	♂	4	October	1969
UF 31001	♂	4	October	1969
UF 31002	♀	4	October	1969
UF 31003	♀	4	October	1969
UF 31004	♀	4	October	1969
UF 31005	♂	4	October	1969
UF 31006	♂	4	October	1969
UF 31031	♂	6	October	1969
UF 31032	♂	6	October	1969
UF 31033	♀	6	October	1969
UF 31056	♂	16	November	1969
UF 31057	♂	16	November	1969
UF 31058	♀	16	November	1969
UF 31068	♂	17	November	1969
UF 31069	♀	17	November	1969
UF 31070	♀	17	November	1969
UF 31092	♂	19	November	1969
UF 31097	♂	20	November	1969
UF 31098	♀	20	November	1969
UF 31099	♀	20	November	1969
UF 31100	♀	20	November	1969
UF 31153	♂	21	November	1969
UF 31156	♂	22	November	1969
UF 31157	♂	22	November	1969
UF 31158	♂	22	November	1969
UF 31159	♂	22	November	1969
UF 31400	♀	18	February	1970
UF 31449	♂	19	February	1970
UF 31575	♂	24	February	1970
UF 31698	♀	5	March	1970
UF 31705	♂	6	March	1970

Anolis capito

UF 30742	♂	10	September	1969
UF 30748	♂	12	September	1969
UF 30811	♂	17	September	1969
UF 30866	♂	21	September	1969
UF 30931	♀	2	October	1969
UF 30967	♂	3	October	1969
UF 31034	♂	6	October	1969
UF 31067	♂	17	November	1969
UF 30867	♂	21	September	1969
UF 31853	♂	25	September	1969
UF 31854	♀	25	September	1969
UF 30930	♀	2	October	1969
UF 31579	♂	26	February	1970
UF 31664	♂	3	March	1970
UF 31697	♂	5	March	1970
UF 31704	♀	6	March	1970

Anolis capito - continued

UF 31084	♂	18 November	1969
UF 31134	♀	20 November	1969
UF 31195	♀	30 November	1969
UF 31522	♀	22 February	1970
UF 31725	♀	7 March	1970
UF 31778	♀	10 March	1970
UF 32326	♂	12 March	1970

Anolis carpenteri

UF 30789	♂	16 September	1969
UF 30808	♂	17 September	1969
UF 30809	♀	17 September	1969
UF 30858	♂	21 September	1969
UF 30859	♀	21 September	1969
UF 30860	♂	21 September	1969
UF 30861	♂	21 September	1969
UF 30862	♀	21 September	1969
UF 30863	♂	21 September	1969
UF 30864	♀	21 September	1969
UF 31857	♂	25 September	1969
UF 30908	♂	1 October	1969
UF 30909	♀	1 October	1969
UF 30910	♀	1 October	1969
UF 30919	♂	2 October	1969
UF 30920	♂	2 October	1969
UF 30921	♀	2 October	1969
UF 30922	♂	2 October	1969
UF 30923	♂	2 October	1969
UF 30924	♀	2 October	1969
UF 30925	♀	2 October	1969
UF 30974	♂	3 October	1969
UF 30975	♂	3 October	1969
UF 30976	♂	3 October	1969
UF 30977	♀	3 October	1969
UF 30978	♀	3 October	1969
UF 30979	♀	3 October	1969
UF 30980	♂	4 October	1969
UF 30981	♂	4 October	1969
UF 30982	♀	4 October	1969
UF 31017	♂	5 October	1969
UF 31018	♀	5 October	1969
UF 31019	♀	5 October	1969
UF 31047	♂	6 October	1969
UF 31048	♀	6 October	1969
UF 31059	♂	16 November	1969
UF 31060	♂	16 November	1969
UF 31085	♂	18 November	1969
UF 31101	♂	20 November	1969
UF 31102	♂	20 November	1969
UF 31152	♂	21 November	1969
UF 31397	♀	18 February	1970
UF 31572	♂	24 February	1970
UF 31695	♂	5 March	1970
UF 31696	♀	5 March	1970
UF 32320	♀	12 March	1970

Anolis humilis

UF 30739	♂	10 September	1969
UF 30740	♀	10 September	1969
UF 30769	♀	14 September	1969
UF 30781	♀	14 September	1969
UF 30782	♂	14 September	1969
UF 30783	♀	14 September	1969
UF 30802	♀	16 September	1969
UF 30803	j	16 September	1969
UF 30812	♂	17 September	1969
UF 30813	♂	17 September	1969
UF 30814	♂	17 September	1969
UF 30815	♂	17 September	1969
UF 30816	♂	17 September	1969
UF 30817	♀	17 September	1969
UF 30818	♀	17 September	1969
UF 30819	♀	17 September	1969
UF 31826	♂	20 September	1969
UF 31827	♀	20 September	1969
UF 31828	♀	20 September	1969
UF 31829	♀	20 September	1969
UF 31830	j	20 September	1969
UF 31831	j	20 September	1969
UF 30854	♀	21 September	1969
UF 30872	j	23 September	1969
UF 30873	j	23 September	1969
UF 31846	♂	24 September	1969
UF 31847	♂	24 September	1969
UF 31848	♀	24 September	1969
UF 31849	♀	24 September	1969
UF 31850	♀	24 September	1969
UF 31851	♂	24 September	1969
UF 31852	j	24 September	1969
UF 31863	♂	25 September	1969
UF 31864	♂	25 September	1969

Anolis humilis - continued

UF	31865	♂	25 September	1969
UF	31866	♂	25 September	1969
UF	31867	♂	25 September	1969
UF	31868	♂	25 September	1969
UF	31869	♀	25 September	1969
UF	31870	♀	25 September	1969
UF	31871	♂	25 September	1969
UF	31872	♂	25 September	1969
UF	31873	j	25 September	1969
UF	30890	♂	26 September	1969
UF	31922	♂	29 September	1969
UF	31923	♀	29 September	1969
UF	31924	j	29 September	1969
UF	31925	j	29 September	1969
UF	31926	j	29 September	1969
UF	31927	j	29 September	1969
UF	31928	j	29 September	1969
UF	31971	♀	30 September	1969
UF	31972	♂	30 September	1969
UF	31973	♀	30 September	1969
UF	31974	j	30 September	1969
UF	31975	j	30 September	1969
UF	30929	♂	2 October	1969
UF	30968	♂	3 October	1969
UF	30969	♀	3 October	1969
UF	31035	♀	6 October	1969
UF	31061	j	16 November	1969
UF	31127	♂	20 November	1969
UF	31128	♀	20 November	1969
UF	31129	♀	20 November	1969
UF	31130	♀	20 November	1969
UF	31131	♂	20 November	1969
UF	31132	♂	20 November	1969
UF	31150	♂	21 November	1969
UF	31151	j	21 November	1969
UF	31163	♂	22 November	1969
UF	31164	♀	22 November	1969
UF	31165	♀	22 November	1969
UF	31188	♂	25 November	1969
UF	31189	♂	25 November	1969
UF	31197	♂	1 December	1969
UF	31198	♀	1 December	1969
UF	31199	j	1 December	1969
UF	31214	♀	4 December	1969
UF	32032	♂	5 December	1969
UF	32033	♂	5 December	1969
UF	32034	♂	5 December	1969
UF	32035	♂	5 December	1969
UF	32036	♀	5 December	1969
UF	32037	♀	5 December	1969
UF	32038	♂	5 December	1969
UF	32039	♂	5 December	1969
UF	32040	♂	5 December	1969
UF	32041	♂	5 December	1969
UF	32042	♂	5 December	1969
UF	32043	♂	5 December	1969
UF	32044	♀	5 December	1969
UF	32045	♀	5 December	1969
UF	32046	j	5 December	1969
UF	32047	j	5 December	1969
UF	32048	j	5 December	1969
UF	32049	j	5 December	1969
UF	32050	j	5 December	1969
UF	32100	♂	7 December	1969
UF	32101	♂	7 December	1969
UF	32102	♀	7 December	1969
UF	32103	♂	7 December	1969
UF	32104	♀	7 December	1969
UF	32105	♀	7 December	1969
UF	32143	♂	9 December	1969
UF	32144	♂	9 December	1969
UF	32145	♂	9 December	1969
UF	32146	♂	9 December	1969
UF	32147	♂	9 December	1969
UF	32148	♀	9 December	1969
UF	32149	♀	9 December	1969
UF	32150	♀	9 December	1969
UF	32151	♀	9 December	1969
UF	32152	j	9 December	1969
UF	32153	j	9 December	1969
UF	32209	♂	11 December	1969
UF	32210	♂	11 December	1969
UF	32211	♂	11 December	1969
UF	32212	♀	11 December	1969
UF	32213	♀	11 December	1969
UF	32214	j	11 December	1969
UF	32258	♂	13 December	1969
UF	32259	♂	13 December	1969
UF	32260	♂	13 December	1969
UF	32261	♂	13 December	1969
UF	32262	♂	13 December	1969
UF	32263	♀	13 December	1969
UF	32264	♀	13 December	1969
UF	32265	♂	13 December	1969
UF	32266	♀	13 December	1969
UF	32267	♂	13 December	1969
UF	32268	j	13 December	1969
UF	32269	♀	13 December	1969
UF	32270	♀	13 December	1969
UF	32271	♀	13 December	1969

Anolis humilis - continued

UF 32272	♀	13	December	1969
UF 32273	j	13	December	1969
UF 32274	j	13	December	1969
UF 32275	j	13	December	1969
UF 31247	j	13	December	1969
UF 31248	j	13	December	1969
UF 31280	♂	11	February	1970
UF 31287	♂	12	February	1970
UF 31288	♀	12	February	1970
UF 31289	j	12	February	1970
UF 31299	♀	13	February	1970
UF 31300	♀	13	February	1970
UF 31301	♀	13	February	1970
UF 13107	♀	15	February	1970
UF 31337	♂	17	February	1970
UF 31338	♀	17	February	1970
UF 31339	♀	17	February	1970
UF 31378	♀	18	February	1970
UF 31398	♂	18	February	1970
UF 31401	♀	19	February	1970
UF 31402	♀	19	February	1970
UF 31403	♀	19	February	1970
UF 31404	♂	19	February	1970
UF 31405	j	19	February	1970
UF 31406	j	19	February	1970
UF 31453	♂	20	February	1970
UF 31469	♀	20	February	1970
UF 31471	♂	21	February	1970
UF 31472	♂	21	February	1970
UF 31473	♀	21	February	1970
UF 31474	♀	21	February	1970
UF 31475	j	21	February	1970
UF 31526	♀	23	February	1970
UF 31527	j	23	February	1970
UF 31528	j	23	February	1970
UF 31570	♀	24	February	1970
UF 31581	♂	26	February	1970
UF 31582	♂	26	February	1970
UF 31597	♂	27	February	1970
UF 31598	♂	27	February	1970
UF 31599	♂	27	February	1970
UF 31600	♀	27	February	1970
UF 31601	♀	27	February	1970
UF 31602	♀	27	February	1970
UF 31603	♀	27	February	1970
UF 31652	♂	2	March	1970
UF 31653	♂	2	March	1970
UF 31654	♂	2	March	1970
UF 31655	♀	2	March	1970
UF 31656	♀	2	March	1970
UF 31657	♀	2	March	1970
UF 31658	♀	2	March	1970
UF 31659	♀	2	March	1970
UF 31660	♂	2	March	1970
UF 31707	♂	6	March	1970
UF 31708	♀	6	March	1970
UF 31727	♀	9	March	1970
UF 31728	♀	9	March	1970
UF 31779	♂	10	March	1970
UF 31780	♀	10	March	1970
UF 31781	♀	10	March	1970
UF 31782	♀	10	March	1970
UF 32325	♂	12	March	1970
UF 32327	♂	5	May	1970
UF 32328	♀	5	May	1970
UF 32329	j	5	May	1970
UF 32330	♀	5	May	1970
UF 32344	♂	7	May	1970
UF 32345	♂	7	May	1970
UF 32346	♂	7	May	1970
UF 32347	♀	7	May	1970
UF 32348	♀	7	May	1970
UF 32376	♀	8	May	1970
UF 32390	♂	9	May	1970
UF 32391	♂	9	May	1970
UF 32392	♂	9	May	1970
UF 32393	♂	9	May	1970
UF 32394	♂	9	May	1970
UF 32395	♂	9	May	1970
UF 32396	♀	9	May	1970
UF 32397	♀	9	May	1970
UF 32398	♀	9	May	1970
UF 32399	♀	9	May	1970
UF 32432	♂	10	May	1970
UF 32433	♀	10	May	1970
UF 32460	♀	10	May	1970
UF 32470	♂	11	May	1970
UF 32477	♂	11	May	1970
UF 32478	♂	11	May	1970
UF 32479	♂	11	May	1970
UF 32480	♂	11	May	1970
UF 32481	♀	11	May	1970
MJC 70-9	♂	12	May	1970
MJC 70-10	⚥	12	May	1970
MJC 70-11	♀	12	May	1970
MJC 70-12	♀	12	May	1970
MJC 70-13	♀	12	May	1970
MJC 70-14	♀	12	May	1970
MJC 70-15	♀	12	May	1970
MJC 70-16	♀	12	May	1970

Anolis humilis - continued

MJC 70-20	♂	13	May	1970
MJC 70-21	♂	13	May	1970
MJC 70-22	♂	13	May	1970
MJC 70-23	♂	13	May	1970
MJC 70-68	♂	14	May	1970
MJC 70-69	j	14	May	1970
MJC 70-78	♂	15	May	1970
MJC 70-79	♂	15	May	1970
MJC 70-80	♂	15	May	1970
MJC 70-81	♀	15	May	1970
MJC 70-82	♀	15	May	1970
MJC 70-83	♀	15	May	1970
MJC 70-84	♀	15	May	1970
MJC 70-85	♀	15	May	1970
MJC 70-86	j	15	May	1970
MJC70-104	♀	16	May	1970
MJC70-105	j	16	May	1970
MJC70-112	♀	16	May	1970
MJC70-113	♀	16	May	1970
MJC70-107	♂	17	May	1970

Anolis lemurinus

UF 30523	♀	5	August	1969
UF 30524	♀	5	August	1969
UF 30525	♂	5	August	1969
UF 30527	♂	5	August	1969
UF 30328	♂	5	August	1969
UF 30331	♂	6	August	1969
UF 30720	♂	8	September	1969
UF 30726	♀	9	September	1969
UF 30727	♀	9	September	1969
UF 30743	♂	10	September	1969
UF 30790	♂	16	September	1969
UF 30791	♂	16	September	1969
UF 30792	♀	16	September	1969
UF 30807	♂	17	September	1969
UF 30865	♂	21	September	1969
UF 30911	♂	1	October	1969
UF 30912	♀	1	October	1969
UF 30913	♀	1	October	1969
UF 30914	♂	1	October	1969
UF 30926	♂	2	October	1969
UF 30927	♂	2	October	1969
UF 30928	♂	2	October	1969
UF 30965	♀	3	October	1969
UF 30966	♂	3	October	1969
UF 30983	♂	4	October	1969
UF 30984	♂	4	October	1969
UF 30985	♂	4	October	1969
UF 30986	♂	4	October	1969
UF 30987	♀	4	October	1969
UF 30988	♂	4	October	1969
UF 30989	♂	4	October	1969
UF 30990	♀	4	October	1969
UF 31015	♀	5	October	1969
UF 31016	♂	5	October	1969
UF 31036	♂	6	October	1969
UF 31037	♂	6	October	1969
UF 31038	♂	6	October	1969
UF 31039	♂	6	October	1969
UF 31040	♂	6	October	1969
UF 31041	♀	6	October	1969
UF 31063	♂	16	November	1969
UF 31064	♀	16	November	1969
UF 31072	♀	17	November	1969
UF 31073	♂	17	November	1969
UF 31074	♂	17	November	1969
UF 31075	♂	17	November	1969
UF 31076	♂	17	November	1969
UF 31077	♂	17	November	1969
UF 31093	♀	19	November	1969
UF 31103	♂	20	November	1969
UF 31104	♂	20	November	1969
UF 31105	♂	20	November	1969
UF 31106	♂	20	November	1969
UF 31107	♂	20	November	1969
UF 31108	♂	20	November	1969
UF 31109	♀	20	November	1969
UF 31133	♂	20	November	1969
UF 31173	♂	22	November	1969
UF 31174	♀	22	November	1969
UF 31175	♀	22	November	1969
UF 31176	♀	22	November	1969
UF 31177	♂	22	November	1969
UF 31178	♀	22	November	1969
UF 31179	♂	22	November	1969
UF 31215	♂	4	December	1969
UF 31229	♀	9	December	1969
UF 32215	♂	11	December	1969
UF 31249	♀	13	December	1969
UF 31306	♂	14	February	1970
UF 31554	♀	23	February	1970

Anolis lemurinus - continued

UF 31555	♀	23 February	1970
UF 31576	♂	24 February	1970
UF 31580	♀	26 February	1970
UF 31593	♂	27 February	1970
UF 31594	♂	27 February	1970
UF 31595	♂	27 February	1970
UF 31596	♀	27 February	1970
UF 31614	♂	28 February	1970
UF 31674	♂	4 March	1970
UF 31675	♂	4 March	1970
UF 31676	♂	4 March	1970
UF 31677	♀	4 March	1970
UF 31678	♀	4 March	1970
UF 31679	♀	4 March	1970
UF 31699	♂	5 March	1970
UF 31700	♂	5 March	1970
UF 31701	♀	5 March	1970
UF 31706	♂	6 March	1970
UF 31721	♂	7 March	1970
UF 31722	♀	7 March	1970
UF 31723	♀	7 March	1970
UF 32331	♂	5 May	1970
UF 32349	♀	7 May	1970
UF 32350	♀	7 May	1970
UF 32377	♂	8 May	1970
UF 32378	♀	8 May	1970
UF 32379	♀	8 May	1970
UF 32400	♀	9 May	1970
UF 32482	♀	11 May	1970
MJC70-17	♂	12 May	1970
MJC70-87	♂	15 May	1970
MJC70-88	♂	15 May	1970
MJC70-114	♂	16 May	1970
MJC70-124	♂	18 May	1970
MJC70-125	♀	18 May	1970

Anolis limifrons

UF 30719	♀	7 September	1969
UF 30722	♀	8 September	1969
UF 30728	♂	9 September	1969
UF 30729	♀	9 September	1969
UF 30735	♂	9 September	1969
UF 30770	♂	14 September	1969
UF 30771	♂	14 September	1969
UF 30772	♂	14 September	1969
UF 30773	♂	14 September	1969
UF 30774	♂	14 September	1969
UF 30775	♀	14 September	1969
UF 30776	♀	14 September	1969
UF 30777	♀	14 September	1969
UF 30778	♀	14 September	1969
UF 30779	♀	14 September	1969
UF 30780	j	14 September	1969
UF 30784	♂	15 September	1969
UF 30785	j	15 September	1969
UF 30793	♂	16 September	1969
UF 30794	♂	16 September	1969
UF 30795	♂	16 September	1969
UF 30796	♂	16 September	1969
UF 30797	♀	16 September	1969
UF 30798	♀	16 September	1969
UF 30799	♀	16 September	1969
UF 30800	♀	16 September	1969
UF 30801	♀	16 September	1969
UF 30820	♂	17 September	1969
UF 30821	♂	17 September	1969
UF 30822	♂	17 September	1969
UF 30823	♂	17 September	1969
UF 30824	♂	17 September	1969
UF 30825	♂	17 September	1969
UF 30826	♂	17 September	1969
UF 30827	♀	17 September	1969
UF 30828	♀	17 September	1969
UF 30829	♀	17 September	1969
UF 30830	♀	17 September	1969
UF 30831	♀	17 September	1969
UF 30832	♀	17 September	1969
UF 30833	♀	17 September	1969
UF 30834	♀	17 September	1969
UF 30835	♀	17 September	1969
UF 30836	♂	17 September	1969
UF 30837	♂	17 September	1969
UF 30838	♂	17 September	1969
UF 30839	♀	17 September	1969
UF 30840	j	17 September	1969
UF 30853	♂	20 September	1969
UF 31820	♂	20 September	1969
UF 31821	♀	20 September	1969
UF 31822	♀	20 September	1969
UF 31823	♀	20 September	1969
UF 31824	j	20 September	1969
UF 31825	j	20 September	1969
UF 30879	♂	24 September	1969
UF 30880	♂	24 September	1969
UF 30881	♀	24 September	1969

Anolis limifrons - continued

UF 30882	♀	24	September	1969
UF 31841	♂	24	September	1969
UF 31842	♂	24	September	1969
UF 31843	♀	24	September	1969
UF 31844	♂	24	September	1969
UF 31845	j	24	September	1969
UF 31860	♂	25	September	1969
UF 31861	♂	25	September	1969
UF 31862	♀	25	September	1969
UF 31894	♀	28	September	1969
UF 31969	♀	30	September	1969
UF 31970	♀	30	September	1969
UF 30905	♂	1	October	1969
UF 30906	♀	1	October	1969
UF 30937	♂	2	October	1969
UF 30938	♂	2	October	1969
UF 30939	♂	2	October	1969
UF 30940	♀	2	October	1969
UF 30941	♀	2	October	1969
UF 30942	♂	2	October	1969
UF 30970	♂	3	October	1969
UF 30971	♂	3	October	1969
UF 30972	♀	3	October	1969
UF 30973	j	3	October	1969
UF 30991	♂	4	October	1969
UF 30992	♂	4	October	1969
UF 30993	♂	4	October	1969
UF 30994	♀	4	October	1969
UF 30995	♀	4	October	1969
UF 30996	♀	4	October	1969
UF 31020	♂	5	October	1969
UF 31021	♀	5	October	1969
UF 31022	♀	5	October	1969
UF 31023	♂	5	October	1969
UF 31042	♂	6	October	1969
UF 31043	♀	6	October	1969
UF 31062	♀	16	November	1969
UF 31071	♀	17	November	1969
UF 31086	♂	18	November	1969
Uf 31087	♂	18	November	1969
UF 31088	♂	18	November	1969
UF 31089	♀	18	November	1969
UF 31094	♂	19	November	1969
UF 31095	♂	19	November	1969
UF 31113	♂	20	November	1969
UF 31114	♂	20	November	1969
UF 31115	♂	20	November	1969
UF 31116	♂	20	November	1969
UF 31117	♂	20	November	1969
UF 31118	♂	20	November	1969
UF 31119	♂	20	November	1969
UF 31120	♂	20	November	1969
UF 31121	♂	20	November	1969
UF 31122	♀	20	November	1969
UF 31123	♀	20	November	1969
UF 31124	♀	20	November	1969
UF 31125	j	20	November	1969
UF 31126	♂	20	November	1969
UF 31145	♂	21	November	1969
UF 31146	♂	21	November	1969
UF 31147	♂	21	November	1969
UF 31148	♂	21	November	1969
UF 31149	♀	21	November	1969
UF 31166	♂	22	November	1969
UF 31167	♂	22	November	1969
UF 31168	♂	22	November	1969
UF 31169	♂	22	November	1969
UF 31170	♀	22	November	1969
UF 31171	♀	22	November	1969
UF 31172	♀	22	November	1969
UF 31182	♂	24	November	1969
UF 31183	♀	24	November	1969
UF 31184	♀	24	November	1969
UF 31186	♂	25	November	1969
UF 31187	♂	25	November	1969
UF 31200	♂	1	December	1969
UF 31201	♂	1	December	1969
UF 31202	♂	1	December	1969
UF 31203	♂	1	December	1969
UF 31204	♀	1	December	1969
UF 31205	♀	1	December	1969
UF 31206	♀	1	December	1969
UF 31207	♀	1	December	1969
UF 31216	♂	4	December	1969
UF 31217	♂	4	December	1969
UF 31218	♂	4	December	1969
UF 31219	♂	4	December	1969
UF 31220	♀	4	December	1969
UF 31221	♀	4	December	1969
UF 32028	♂	5	December	1969
UF 32029	♂	5	December	1969
UF 32030	♂	5	December	1969
UF 32031	j	5	December	1969
UF 32095	♂	7	December	1969
UF 32096	♂	7	December	1969
UF 32097	♂	7	December	1969
UF 32098	♀	7	December	1969
UF 32099	♀	7	December	1969
UF 32207	♀	11	December	1969
UF 32208	j	11	December	1969

Anolis limifrons - continued

UF 32252	♂	13 December	1969
UF 32253	♀	13 December	1969
UF 32254	♀	13 December	1969
UF 32255	♀	13 December	1969
UF 32256	♂	13 December	1969
UF 32257	j	13 December	1969
UF 31296	♂	13 February	1970
UF 31297	♀	13 February	1970
UF 31298	♂	13 February	1970
UF 31340	♂	17 February	1970
UF 31341	♀	17 February	1970
UF 31342	♀	17 February	1970
UF 31343	♂	17 February	1970
UF 31344	♀	17 February	1970
UF 31399	♂	18 February	1970
UF 31407	♂	19 February	1970
UF 31408	♂	19 February	1970
UF 31476	♂	21 February	1970
UF 31477	♀	21 February	1970
UF 31478	♀	21 February	1970
UF 31479	♂	21 February	1970
UF 31480	j	21 February	1970
UF 31506	♀	21 February	1970
UF 31507	♀	21 February	1970
UF 31508	♀	21 February	1970
UF 31509	♀	21 February	1970
UF 31510	♀	21 February	1970
UF 31511	♀	21 February	1970
UF 31512	j	21 February	1970
UF 31513	♂	21 February	1970
UF 31514	j	21 February	1970
UF 31515	j	21 February	1970
UF 31516	j	21 February	1970
UF 31529	♂	23 February	1970
UF 31530	♂	23 February	1970
UF 31531	♂	23 February	1970
UF 31532	♀	23 February	1970
UF 31533	j	23 February	1970
UF 31556	♂	23 February	1970
UF 31557	♂	23 February	1970
UF 31558	♂	23 February	1970
UF 31559	♀	23 February	1970
UF 31560	♀	23 February	1970
UF 31561	♀	23 February	1970
UF 31562	♀	23 February	1970
UF 31563	♀	23 February	1970
UF 31564	♀	23 February	1970
UF 31565	♀	23 February	1970
UF 31566	♀	23 February	1970
UF 31567	j	23 February	1970
UF 31571	♀	24 February	1970
UF 31573	♂	24 February	1970
UF 31583	♀	26 February	1970
UF 31584	♀	26 February	1970
UF 31585	j	26 February	1970
UF 31589	♀	27 February	1970
UF 31590	j	27 February	1970
UF 31604	♂	27 February	1970
UF 31605	♀	27 February	1970
UF 31606	♀	27 February	1970
UF 31644	♂	1 March	1970
UF 31662	♀	2 March	1970
UF 31663	♀	2 March	1970
UF 31666	♀	3 March	1970
UF 31680	♀	4 March	1970
UF 31702	♀	5 March	1970
UF 31724	♂	7 March	1970
UF 31753	♂	9 March	1970
UF 31754	♂	9 March	1970
UF 31755	♂	9 March	1970
UF 31756	♀	9 March	1970
UF 31757	♀	9 March	1970
UF 31765	♂	10 March	1970
UF 31766	♂	10 March	1970
UF 31767	♂	10 March	1970
UF 31768	♂	10 March	1970
UF 31769	♂	10 March	1970
UF 31770	♂	10 March	1970
UF 31771	♀	10 March	1970
UF 31772	♀	10 March	1970
UF 31773	♀	10 March	1970
UF 31774	♀	10 March	1970
UF 31775	♀	10 March	1970
UF 31776	♀	10 March	1970
UF 31777	♀	10 March	1970
UF 32321	♂	12 March	1970
UF 32322	♂	12 March	1970
UF 32323	♂	12 March	1970
UF 32324	♀	12 March	1970
UF 32332	♂	5 May	1970
UF 32333	♂	5 May	1970
UF 32334	♂	5 May	1970
UF 32335	j	5 May	1970
UF 32343	♂	6 May	1970
UF 32351	♀	7 May	1970
UF 32352	♂	7 May	1970
UF 32358	♂	8 May	1970
UF 32359	♀	8 May	1970
UF 32380	♀	8 May	1970
UF 32381	♀	8 May	1970

Anolis limifrons - continued

UF 32401	♂	9 May	1970
UF 32402	♂	9 May	1970
UF 32403	♂	9 May	1970
UF 32404	♂	9 May	1970
UF 32405	♂	9 May	1970
UF 32406	♂	9 May	1970
UF 32407	♂	9 May	1970
UF 32408	♂	9 May	1970
UF 32409	♂	9 May	1970
UF 32410	♀	9 May	1970
UF 32411	♂	9 May	1970
UF 32412	♂	9 May	1970
UF 32413	♀	9 May	1970
UF 32414	♀	9 May	1970
UF 32415	♀	9 May	1970
UF 32416	♀	9 May	1970
UF 32417	♀	9 May	1970
UF 32418	♀	9 May	1970
UF 32419	♀	9 May	1970
UF 32420	♀	9 May	1970
UF 32421	♀	9 May	1970
UF 32422	j	9 May	1970
UF 32423	♀	9 May	1970
UF 32424	♀	9 May	1970
UF 32425	♀	9 May	1970
UF 32426	♀	9 May	1970
UF 32427	j	9 May	1970
UF 32428	j	9 May	1970
UF 32434	♀	10 May	1970
UF 32461	♂	10 May	1970
UF 32462	♂	10 May	1970
UF 32463	♂	10 May	1970
UF 32464	♀	10 May	1970
UF 32465	♀	10 May	1970
UF 32466	♀	10 May	1970
UF 32467	♀	10 May	1970
UF 32468	♀	10 May	1970
UF 32469	♂	10 May	1970
UF 32483	♂	11 May	1970
UF 32484	♂	11 May	1970
UF 32485	♂	11 May	1970
UF 32486	♂	11 May	1970
UF 32487	♂	11 May	1970
UF 32488	♂	11 May	1970
UF 32489	♀	11 May	1970
UF 32490	♀	11 May	1970
UF 32491	♀	11 May	1970
UF 32492	♀	11 May	1970
UF 32493	♀	11 May	1970
UF 32494	♀	11 May	1970
UF 32495	♀	11 May	1970
UF 32496	♀	11 May	1970
UF 32497	j	11 May	1970
UF 32498	♂	11 May	1970
UF 32499	♂	12 May	1970
UF 32500	♂	12 May	1970
MJC70-1	♀	12 May	1970
MJC70-2	♀	12 May	1970
MJC70-3	j	12 May	1970
MJC70-18	♂	12 May	1970
MJC70-24	♂	13 May	1970
MJC70-25	♂	13 May	1970
MJC70-26	♂	13 May	1970
MJC70-27	♂	13 May	1970
MJC70-28	♂	13 May	1970
MJC70-29	♂	13 May	1970
MJC70-30	♂	13 May	1970
MJC70-31	♂	13 May	1970
MJC70-32	♀	13 May	1970
MJC70-33	♀	13 May	1970
MJC70-34	♀	13 May	1970
MJC70-35	♀	13 May	1970
MJC70-36	♀	13 May	1970
MJC70-37	♀	13 May	1970
MJC70-38	♀	13 May	1970
MJC70-66	♂	14 May	1970
MJC70-67	♀	14 May	1970
MJC70-71	♂	15 May	1970
MJC70-89	♂	15 May	1970
MJC70-90	♂	15 May	1970
MJC70-91	♂	15 May	1970
MJC70-92	♂	15 May	1970
MJC70-93	♂	15 May	1970
MJC70-94	♀	15 May	1970
MJC70-95	♀	15 May	1970
MJC70-96	♀	15 May	1970
MJC70-97	♀	15 May	1970
MJC70-98	♀	15 May	1970
MJC70-99	j	15 May	1970
MJC70-103	♂	16 May	1970
MJC70-115	♂	16 May	1970
MJC70-116	♂	16 May	1970
MJC70-117	♂	16 May	1970
MJC70-108	♂	17 May	1970
MJC70-109	♂	17 May	1970

Anolis lionotus

UF 30753	♂	13	September	1969
UF 30754	♂	13	September	1969
UF 30755	♂	13	September	1969
UF 30756	♀	13	September	1969
UF 30757	♂	13	September	1969
UF 31251	♂	14	December	1969
UF 31252	♂	15	December	1969
UF 31253	♀	14	December	1969
UF 31254	♀	14	December	1969
UF 31255	♂	14	December	1969
UF 31256	♀	14	December	1969
UF 31257	♀	14	December	1969
UF 31258	♀	14	December	1969
UF 31259	♀	14	December	1969
UF 31260	♀	14	December	1969
UF 31261	♂	14	December	1969
UF 31262	♀	14	December	1969
UF 31263	♂	14	December	1969
UF 31264	♀	14	December	1969
UF 31468	♂	20	February	1970
UF 31621	♂	1	March	1970
UF 31622	♂	1	March	1970
UF 31623	♂	1	March	1970
UF 31624	♂	1	March	1970
UF 31625	♂	1	March	1970
UF 31626	♂	1	March	1970
UF 31627	♂	1	March	1970
UF 31628	♂	1	March	1970
UF 31629	♀	1	March	1970
UF 31630	♀	1	March	1970
UF 31631	♀	1	March	1970
UF 31632	♀	1	March	1970
UF 31633	♀	1	March	1970
UF 31634	♀	1	March	1970
UF 31635	♀	1	March	1970
UF 31636	♀	1	March	1970
UF 31637	♀	1	March	1970
UF 31638	♀	1	March	1970
UF 31639	♀	1	March	1970
UF 31640	♀	1	March	1970
UF 31641	♂	1	March	1970
UF 31642	♂	1	March	1970
UF 31643	♂	1	March	1970
UF 31729	♂	9	March	1970
UF 31730	♂	9	March	1970
UF 31731	♂	9	March	1970
UF 31732	♂	9	March	1970
UF 31733	♂	9	March	1970
UF 31734	♂	9	March	1970
UF 31735	♂	9	March	1970
UF 31736	♂	9	March	1970
UF 31737	♂	9	March	1970
UF 31738	♂	9	March	1970
UF 31739	♂	9	March	1970
UF 31740	♀	9	March	1970
UF 31741	♀	9	March	1970
UF 31742	♀	9	March	1970
UF 31743	♀	9	March	1970
UF 31744	♀	9	March	1970
UF 31745	♀	9	March	1970
UF 31746	♀	9	March	1970
UF 31747	♀	9	March	1970
UF 31748	♀	9	March	1970
UF 31749	♂	9	March	1970
UF 31750	♀	9	March	1970
UF 31751	♂	9	March	1970
UF 31752	♀	9	March	1970
UF 32429	♂	9	May	1970
MJC70-19	♂	12	May	1970
MJC70-39	♂	13	May	1970
MJC70-40	♀	13	May	1970
MJC70-100	♂	15	May	1970
MJC70-101	♀	15	May	1970
MJC70-118	♂	16	May	1970
MJC70-119	♂	16	May	1970
MJC70-120	♂	16	May	1970
MJC70-121	♀	16	May	1970

Anolis pentaprion

Uf 30804	♀	16	September	1969
UF 30810	♀	17	September	1969
UF 30907	♀	1	October	1969
UF 30943	♂	2	October	1969
UF 30944	♂	2	October	1969
UF 30945	♀	2	October	1969
UF 30946	♀	2	October	1969
UF 30947	♀	2	October	1969
UF 31044	♂	6	October	1969
UF 31045	♂	6	October	1969
UF 31046	♂	6	October	1969
UF 31055	♀	16	November	1969
UF 31078	♀	17	November	1969
UF 31079	♀	17	November	1969
UF 31091	♂	19	November	1969
UF 31110	♀	20	November	1969

Anolis pentaprion - continued

UF 31111	♂	20	November	1969
UF 31112	♂	20	November	1969
UF 31160	♂	22	November	1969
UF 31161	♀	22	November	1969
UF 31162	♀	22	November	1969
UF 31304	♀	14	February	1970
UF 31552	♂	23	February	1970
UF 31592	♂	27	February	1970
UF 31665	♂	3	March	1970
UF 32353	♀	7	May	1970

Leiolopisma cherriei

UF 30762	14	September	1969
UF 30763	14	September	1969
UF 30884	24	September	1969
UF 31832	24	September	1969
UF 31858	25	September	1969
UF 31976	30	September	1969
UF 31211	4	December	1969
UF 31212	4	December	1969
UF 32051	5	December	1969
UF 32106	7	December	1969
UF 32107	7	December	1969
UF 32154	9	December	1969
UF 32155	9	December	1969
UF 32156	9	December	1969
UF 31234	10	December	1969
UF 31238	11	December	1969
UF 31246	13	December	1969
UF 32276	13	December	1969
UF 32277	13	December	1969
UF 32278	13	December	1969
UF 31481	21	February	1970
UF 31482	21	February	1970
UF 31588	27	February	1970
UF 31649	2	March	1970
UF 31650	2	March	1970
UF 31651	2	March	1970
UF 32336	5	May	1970
UF 32360	8	May	1970
UF 32435	10	May	1970
UF 32458	10	May	1970
MJC 70-5	12	May	1970
MJC 70-5	12	May	1970
MJC 70-6	12	May	1970
MJC 70-7	12	May	1970
MJC 70-8	12	May	1970
MJC 70-70	14	May	1970
MJC 70-72	15	May	1970
MJC 70-122	16	May	1970
MJC 70-123	16	May	1970

Lepidoblepharis xanthostigma

UF 30764	14	September	1969
UF 30805	16	September	1969
UF 30852	21	September	1969
UF 30870	23	September	1969
UF 31977	30	September	1969
UF 31978	30	September	1969
UF 31196	30	November	1969
UF 32052	5	December	1969
UF 32053	5	December	1969
UF 32054	5	December	1969
UF 32108	7	December	1969
UF 32109	7	December	1969
UF 32110	7	December	1969
UF 32111	7	December	1969
UF 31244	13	December	1969
UF 31245	13	December	1969
UF 32279	13	December	1969
UF 32280	13	December	1969
UF 31302	13	February	1970
UF 31345	17	February	1970
UF 31379	18	February	1970
UF 31518	22	February	1970
UF 32337	5	May	1970
MJC 70-63	14	May	1970
MJC 70-110	17	May	1970
MJC 70-111	17	May	1970

Lepidophyma flavimaculatum

UF 30850	♀	18	September	1969
UF 30869	♀	23	September	1969
UF 30887	♂	25	September	1969
UF 31979	♀	30	September	1969

Lepidophyma flavimaculatum - continued

UF 31980	♀	30	September	1969
UF 31210	♀	4	December	1969
UF 32055	♂	5	December	1969
UF 32056	♀	5	December	1969
UF 32057	♀	5	December	1969
UF 32058	♂	5	December	1969
UF 32059	♀	5	December	1969
UF 32060	♀	5	December	1969
UF 32112	♀	7	December	1969
UF 32217	♀	11	December	1969
UF 31243	♀	13	December	1969
UF 32281	♀	13	December	1969
UF 32282	♀	13	December	1969
UF 32283	♂	13	December	1969
UF 32284	♀	13	December	1969
UF 32285	♀	13	December	1969
UF 32286	♀	13	December	1969
UF 31281	♀	12	February	1970
UF 31282	♀	12	February	1970
UF 31283	♀	12	February	1970
UF 31284	♀	12	February	1970
UF 31285	♂	12	February	1970
UF 31286	♀	12	February	1970
UF 31396	♀	18	February	1970
UF 31517	♀	22	February	1970
UF 32382	♀	8	May	1970
UF 32383	♀	8	May	1970
UF 32436	♀	10	May	1970
UF 32437	♂	10	May	1970
MJC70-106	♂	2	June	1970
MJC70-255	♂	2	June	1970
MJC70-256	♀	2	June	1970

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Michael Jon Corn was born on October 25, 1944, in Mattoon, Illinois. He attended public schools in Charleston and Mattoon, Illinois, graduating from Mattoon Community High School in 1962. He attended Eastern Illinois University, majoring in zoology, minoring in botany, and graduating with the degree Bachelor of Science in Education in 1966. He completed the Master of Science degree at Eastern Illinois University in 1967, also with a zoology major. His thesis was entitled: "A Check-list and Keys to the Primitive Subfamilies of Cerambycidae of Illinois."

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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